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UNITED STATES DEPARTMENT OF AGRICULTURE

BULLETIN No. 700

Contribution from the Forest Service
HENRY S. GRAVES, Forester

Washington, D. C. PROFESSIONAL PAPER October 14, 1918

# CLIMATE AND PLANT GROWTH IN CERTAIN VEGETATIVE ASSOCIATIONS

By

ARTHUR W. SAMPSON, Plant Ecologist
Forest Service

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By ARTHUR W. SAMPSON, *Plant Ecologist, Forest Service.*[1]

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## THE PROBLEM.

The relation of climate to the growth and development of vegetation is of profound importance in both practical and experimental agriculture. It is extremely useful to know the cause of successful growth and establishment, or of partial success or failure, of various species in different plant associations and under widely contrasted climatic conditions. The climatic requirements of various plant types are largely responsible for the results obtained in the case of experimental seedings and plantings of most species. Once the adverse climatic factors are definitely known, failures with plants may be largely avoided by the judicious selection of sites or of species especially adapted to withstand the limiting factors. Therefore, a series of experiments was undertaken, (a) to obtain a comparison of the climatic requirements of the main plant types, and (b) to determine, quantitatively, the relation between various environmental factors on the one hand and plant growth and certain other physiological functions on the other. The results obtained appear to be conclusive in most instances and should prove of value both in experimental and in practical agriculture and forestry.

[1] The author is indebted to F. Merrill Hildebrandt for material assistance in procuring and assembling the data presented in this paper.

It is a matter of common knowledge that the life cycle and structural characteristics of plants are largely determined by the climatic conditions prevailing in the habitat, but the quantitative relations existing between the potent climatic factors and the vegetative activities are not well known. Though the ecologist and plant geographer have shown that a given plant association may have well-defined geographical limits,[1] which in turn are characterized by rather distinct complexes of environmental (climatic) conditions, they have not as yet definitely determined which climatic factor, or set of factors, is most influential in affecting distribution, growth, and physiological activities generally.[2] This is attributable to several conditions. In the first place, the relation of plant development to environment is exceedingly complicated and can be determined quantitatively only when the most influential physical factors are recognized, recorded, and properly interpreted. Secondly, the climatic factors of a given habitat, and, indeed, of different habitats, which have to do with the limitation of the life process, are in themselves more or less indefinite; they are highly complicated and variable, and their intensity can not always be measured fully by instruments. In the third place, methods have not been sufficiently advanced to warrant serious investigations. Owing to present lack of knowledge of the response of plant activities to climate, there is wide diversity of opinion as to how best to summarize and integrate climatic data. Temperature studies conducted by Livingston,[3] Lehenbauer,[4] Merriam,[5] and McLean,[6] and researches on soil humidity and "growth water" carried out by Briggs and Shantz,[7] Shreve,[8] Fuller,[9] and others have shown that climatic factors can not to advantage be expressed empirically. Suitable methods of integrating the potent climatic factors, as well as of recording growth and other plant func-

[1] Drude, O. Entwurf einer biologischen Eintheilung der Gewächse. (A. Shenk, Handbuch der Botanik, III, p. 487.)

[2] As a preliminary study it would be desirable to reduce the complexes of the environmental factors to their simplest form, which, under controlled conditions, might be accomplished by maintaining constant all but the factor investigated, and in this way determining the effectiveness of each. This being done, however, the combined influence would have to be integrated in order to approach conditions in nature. Further, since under natural conditions climatic factors vary widely, both in intensity and in duration, such important variations must necessarily be included in the equation.

[3] Livingston, B. E. and G. J., Temperature coefficients in plant geography and climatology. Bot. Gaz. 56: 346–375. 1913.

[4] Lehenbauer, P. A., Growth of maize seedlings in relation to temperature. Physiol. Res. 1: 247–288. 1914.

[5] Merriam, C. Hart, Laws of temperature control of the geographic distribution of plants and animals. Natl. Geog. Mag. 6: 229–238. 1894.

[6] McLean, F. T., A preliminary study of climatic conditions in Maryland, as related to plant growth. Physiol. Res. 2: 129–207. 1917.

[7] Briggs, Lyman J., and Shantz, H. L., The wilting coefficient for different plants and its direct determination. U. S. Dept. Agr. Bul. No. 230: 7–77. 1912.

[8] Shreve, F., Rainfall as a determinant of soil moisture. Plant World. 17: 9–26. 1914.

[9] Fuller, George D., Evaporation and soil moisture as related to the succession of plant associations. Bot. Gaz., 58: 193–234. 1914.

tions of comparable or "standard" plants developed under the particular climatic conditions summarized, are essential steps in a successful investigation

## THE EXPERIMENTS.

The investigations here reported were conducted in the vicinity of the Great Basin Forest Experiment Station, located on that part of the Wasatch Mountains embraced by the Manti National Forest in central Utah. Here, from the foothills to the highest elevations, between altitudes of approximately 7,000 and 11,000 feet, three distinct plant associations (identical in this locality with vegetative types or life zones) occur. In the heart of each of these associations a type station was selected in 1913. From 1913 to 1916 the more important environmental factors were recorded, and, accordingly, the climatic characteristics of each type-zone are well known. The investigation of the influence of the weather upon the development of comparable plants, with which the present paper is chiefly concerned, was begun in 1915 and continued and extended in 1916. The types here recognized and their approximate altitudinal limits are as follows:

| | | |
|---|---|---|
| Sagebrush–rabbit-brush association | feet | 5,200– 6,500 |
| Oak-brush association | do | 6,500– 7,800 |
| Aspen-fir association | do | 7,500– 9,500 |
| Spruce-fir association | do | 9,000–11,000 |

As indicated by the plants typifying the respective associations, all but the lowest are forested. No special investigations were conducted in the treeless type.

The meteorological stations are located at elevations of 7,100, 8,700, and 10,000 feet. They are all in the same canyon, and the distance between the lowest and the highest stations in an air line is approximately 5 miles. Owing to the possibility of the results being influenced by the presence of trees and other objects in the vicinity of the physical instruments and growing plants, the stations are all located in the open, on slopes dipping slightly to the south, and no vegetation is so close as to cast shadows on the instruments or potometers, except for a few minutes at sunrise and sunset. Also, the instruments and plants are placed as near together as practicable (each type station covering one twenty-fifth of an acre), so that the conditions recorded may be practically identical with those acting upon the plants.

The investigations have been concerned chiefly with (1) recording and summarizing the meteorological data, and (2) determining the relation of certain potent weather factors to growth, water requirement, and certain other physiological functions of standard plants developed under different climatic conditions. Measurements of

growth and certain other activities were recorded from time to time throughout the season. The plants used in each station were a pedigreed strain of Canadian field pea (*Pisum arvense*) known as the Kaiser variety, cultivated wheat (*Triticum durum*) known as Kubanka No. 1440, and mountain brome grass (*Bromus marginatus*) native to the Rocky Mountains. The seed was supplied by the United States Department of Agriculture and was of good viability.

## PREPARATION OF PLANTS.

In 1915 seed of the plants grown in the three type stations as climatic "integrating instruments" was planted directly in potometers, without previous germination. In order to insure as prompt and uniform germination as possible, the seed, prior to planting, was soaked for 36 hours in water of approximately 65° F. The object of this was to start the plants at as nearly the zero point of growth and development as possible.

Direct seeding, however, did not prove entirely satisfactory, chiefly because of the lack of uniformity in size and vigor of the resulting sprouts. In the absence of a known method of selecting seeds which would produce comparable plants, the seed used in obtaining standard plants for investigations in 1916 was first germinated and then such sprouts as appeared to be of the same size and vigor were selected for planting. The sprouts were secured by a method which was a modification of the methods employed by Schreiner and Skinner[1] and other workers of the United States Bureau of Soils. The procedure was as follows: The seeds were disinfected for 15 minutes in a 1 to 500 solution of formaldehyde in water. Following this they were washed thoroughly and soaked for 36 hours at about 65° F., and then placed in a germinator consisting of a bed of sand over which two moist blotters were laid. The soaked seeds were placed between the blotters and a constant water level was maintained in the bed of sand, by means of a Marriotte flask, at such a point that the blotters were kept well moistened but not flooded.

When the radicle was well formed the germinating seed was transferred to a second germinator. This consisted of a circular graniteware pan, 12 inches in diameter and 4 inches deep, the surface of which was covered with waxed (mosquito bar) netting held slightly above the surface of the pan by a glass rod 5 mm. in diameter, so bent as to form a frame. Into the pan a continuous flow of tapwater, the surface of which touched the netting, but never flooded it, was allowed to run. The radicles were inserted through the mesh, leaving the body of the seed partly dry. When the shoot had de-

[1] Schreiner, O., and Skinner, J. J. Some effects of a harmful organic soil constituent. U. S. Dept. Agr. Bur. Soils Bul. 70, 1910.

veloped to a length of about 2½ inches the seedlings were transferred to the receptacles in which they were grown to maturity or until killed by frost.

## PLANTING.

In order to insure luxuriant and healthy development of the plants, those observed throughout the season were grown in substantial heavy galvanized iron potometers.

To protect them from injury by animals, hail, etc., the plants were grown under wire screen of the mesh usually used on screen doors, supported by light wooden frames. These screen frames decreased the light intensity between 40 and 50 per cent.

Water was added to the potometers as needed, the need being determined by the weight of the cans. In no case was the soil allowed to dry to a point approaching closely its wilting coefficient, nor was it at any time flooded. In watering, the potometer was brought up to its original weight. The first watering was done about a month after planting and the second 15 days later. From then on it became necessary to add water about once a week in all stations and oftener in the drier situations.

### THE POTOMETERS.

The potometers were 17 inches high and 14 inches in diameter, and had a capacity of 90 pounds of air-dry soil, which provided a soil mass at all times affording ample space for the proper development and spread of the roots. The cans were fitted with lids of the same material as the cans, and five holes, ¾ of an inch in diaamter, were punched in each for the plants. (Fig. 1, top view.) In the center of the cover a hole 1½ inches in diameter was provided, which was used in watering and was fitted with a cork stopper and a capillary tube bent at right angles.

Before placing the lid, sufficient soil was removed in the center of the can to make room for a granite-ware receptacle 4 inches in height by 5 inches in diameter, perforated centrally in the bottom and underlaid with 1½ inches of gravel, as shown in the sectional view of figure 1. This greatly facilited the addition of water. To add the water, a flask of known capacity was inverted and the water permitted gradually to percolate into the soil.

After the lids were placed, the spaces between the rims and cans were closed by securely sealing them over with strips of surgeon's adhesive tape 2½ inches in width. The adhesive tape was then coated with shellac to prevent its loosening when wetted by rain. The method used in sealing and watering the plants was one devised by Briggs and Shantz,[1] modified somewhat to suit special conditions.

[1] Briggs, Lyman J., and Shantz, H. L. The water requirements of plants. U. S. Dept. Agr. Bur. Plant Ind. Bul. 284: 8–14. 1913.

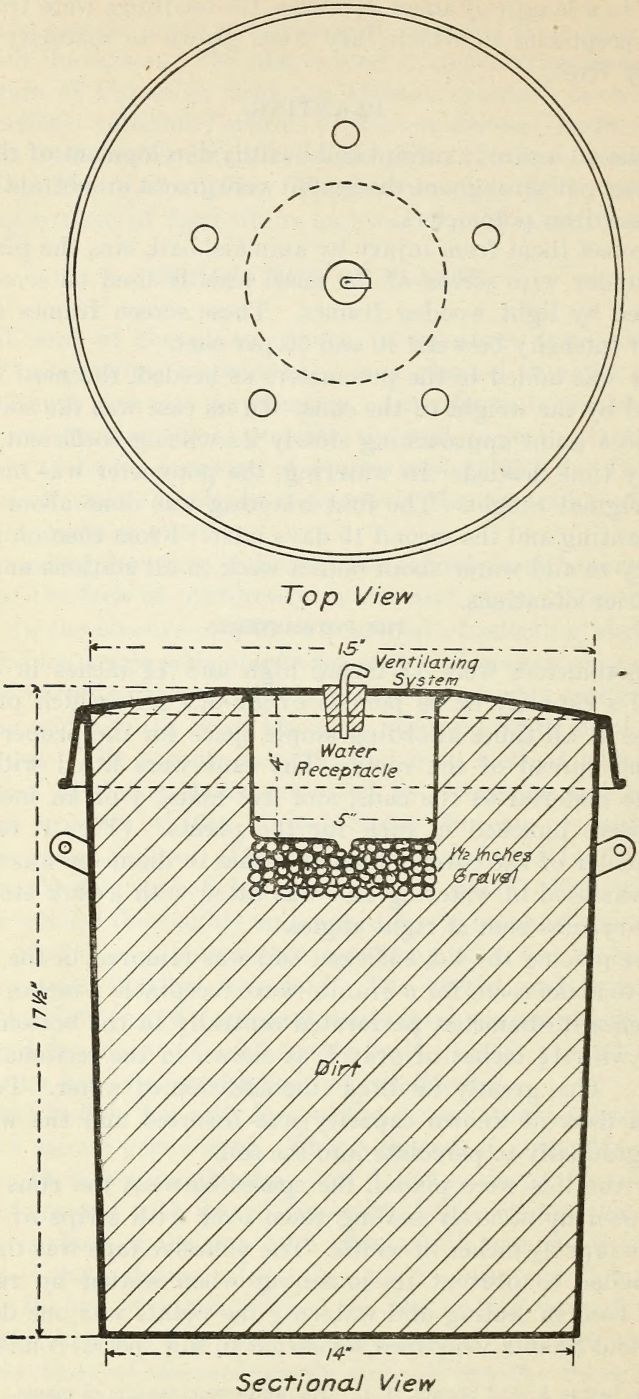


FIG. 1.—Potometer used in growing plants to determine their water requirements.

### THE SOIL.

The soil surface exposed by the perforations in the lids was protected from evaporation by a thin layer of wax consisting of a mixture of 3 parts of tallow and 7 parts of beeswax, applied in a melted condition.

The soil of the region is, in the main, of limestone origin, consequently soil of that type was selected. Except for the purpose of determining the relation of plant growth to soil fertility the soil used was taken from the upper 6 inches in a single situation in the aspen-fir type, and was uniform throughout all the potometers. In order to eliminate pebbles, roots, and other decomposed organic matter the soil was sifted through a $\frac{1}{4}$-inch wire mesh. Because of the presence of a large amount of clay the native soil is not so porous as was desired, and for this reason sand was mixed with it in the proportion of 5 parts of soil to 1 part of sand. The soil used was rich in humus, 5 samples averaging 12 per cent by weight after mixing with the sand. The addition of the sand reduced the wilting coefficient somewhat, the average being approximately 15 per cent.

After the soil was thoroughly mixed in the air-dry state, water was sprinkled over it until it had a "fresh" consistency; that is, the particles adhered in a lump when squeezed in the hand. Soil samples taken from each batch of soil after mixing and watering were found to average 31 per cent humidity, the variation being from 28 to 34 per cent. The moist soil was moderately tamped in the potometers, so as to prevent breaking of the roots by cracking and settling of the soil when drying. The weight of the moist soil in the potometers averaged 135 pounds.

### EFFECT OF SOIL FERTILITY ON WATER REQUIREMENTS AND GROWTH.

While it has long been known that the development of the plant and the amount of water required for the production of a unit of dry matter may vary widely according to the texture and fertility of the soil,[1] it was deemed advisable to determine the difference in water requirements and growth of plants developed in soils of the same origin and texture, but differing appreciably in organic matter. The two soils investigated were of limestone origin and formed within 50 yards of each other in the spruce-fir type at about 10,000 feet elevation. They may be briefly described as follows:

(1) Infertile clay loam. The soil was well disintegrated, but owing to the destruction of most of the ground cover erosion and washing had diminished the humus content and to some extent the soluble salts.

[1] Sachs, J., Bericht über die physiologische Thätigskeit an der Versuchsstation in Tharandt. Landwirthschaftlichen Versuchsstationen. Vol. 1: 235. 1859.

(2) Fertile clay loam. This was of the same general texture as the less fertile soil, but owing to the presence of an adequate ground cover the soil had not been subject to washing and erosion. It appeared to be more mellow than the "infertile" clay loam and was darker in color.

The more important chemical properties at the time of the beginning of the experiment were as follows:

| Soil. | Lime (CaO). | Potash ($K_2O$). | Phosphoric acid ($P_2O_5$). | Total nitrogen. | Loss by ignition. |
|---|---|---|---|---|---|
| | *Per cent.* | *Per cent.* | *Per cent.* | *Per cent.* | *Per cent.* |
| Infertile clay loam | 1.23 | 1.53 | 0.22 | 0.156 | 6.64 |
| Fertile clay loam | 1.49 | 1.30 | .33 | .488 | 14.65 |

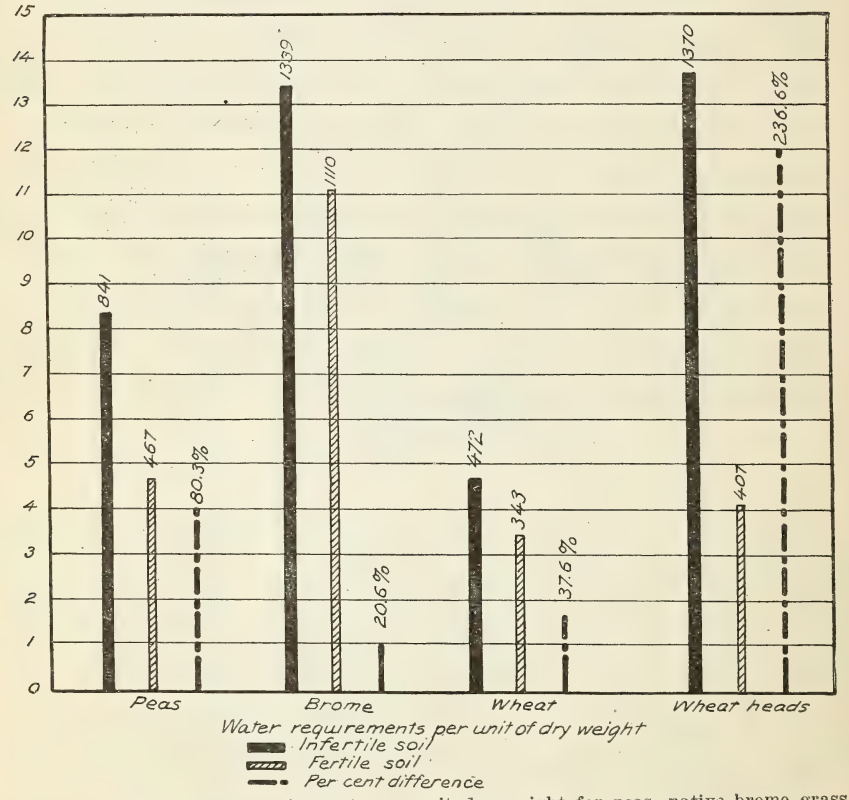


FIG. 2.—Relative water requirements per unit dry weight for peas, native brome grass, and wheat grown in infertile and in fertile soils of the same type.

The chief difference chemically was in the total nitrogen content. Also there was a wide difference in the humus content as determined by incineration. The difference in the latter was largely responsible for the contrast in the wilting coefficients of the soils, this factor

being 19.3 per cent in the fertile loam soil and 15.6 per cent in the infertile loam.

After sifting and preparing the soils for the reception of the plants according to the procedure previously described, two hermetically sealed batteries of each soil type were planted with sprouts of wheat of about equal leaf area and thrift, two with Canadian field peas, and one each with mountain brome grass. Thus 10 plants each of wheat and peas, and 5 of brome grass were grown in each soil type. The potometers were placed in the meteorological station of the aspen-fir type, where the plants were grown until inclement weather set in in the autumn.

The water requirements for the production of a unit of dry matter of field peas, mountain brome grass, wheat, and wheat heads in the two soils are shown in Table 1, and graphically in figure 2.

TABLE 1.—*Water requirement in grams of peas, brome grass, wheat, and wheat heads per gram of dry matter.*

| Soil. | Peas. | Brome grass. | Wheat. | Wheat heads. |
|---|---|---|---|---|
| Infertile soil | 841 | 1,339 | 472 | 1,370 |
| Fertile soil | 467 | 1,110 | 343 | 407 |
| Per cent difference | 80.3 | 20.6 | 37.6 | 236.6 |

In all cases notably more water was required for the production of a unit of dry matter in the infertile loam soil than in the fertile loam. The difference was greater in the peas than in the brome grass or the wheat. The brome grass was less influenced than either wheat or peas. The greatest difference occurred in the production of wheat heads, there being a requirement of 237 per cent more in the infertile than in the fertile soil. Under natural conditions brome grass grows in soils of relatively low fertility, and the species succeeds in completing its life cycle in soils similar to the infertile soil here experimented with.

In summing up the total water used by the plants grown in the two selected soils it was found that a great deal more was consumed by the plants grown in the fertile than in the infertile soil, despite the fact that much more water was required by the plants grown in the infertile soil per unit of dry matter.

It is noteworthy that a wide variation exists between the water requirement per unit of dry matter of brome grass and that of peas and wheat, even when the plants are grown in the *same sort of soil.* Thus in the case of the fertile soil brome grass uses more than twice as much water as the other two species, while in the infertile soil the ratio is practically the same.[1] This wide difference in water require-

[1] For a review of literature bearing on the subject, see Briggs, L. J., and Shantz, H. L. The Water Requirements of Plants, II. A Review of the Literature. U. S. Dept. of Agr. B. P. I. Bull. 285. 1913.

ment led to an examination of the character and extent of the root systems of the species in question. The examinations showed that the extent of root system varied widely, as is shown in Table 2, and figure 3.

TABLE 2.—*Relation of aerial and subterranean parts of peas, wheat, and brome grass, and comparative water requirements of aerial growth and of aerial and root development combined.*

| Plant. | Weight of roots. | Weight of tops. | Ratio of roots to tops. | Water requirement per gram of dry matter. | Water requirement per gram of dry matter including roots. |
|---|---|---|---|---|---|
| | *Grams.* | *Grams.* | *Per cent.* | *Grams.* | *Grams.* |
| Peas | 7.00 | 231.31 | 3.03 | 368 | 358 |
| Wheat | 8.70 | 264.92 | 3.3 | 358 | 279 |
| Brome grass | 12.82 | 60.11 | 21.3 | 516 | 413 |

Table 2 shows that the dry weight of the roots of peas was approximately 3 per cent of the dry weight of the tops, and the roots of wheat about 3.3 per cent; in the case of the brome grass the roots weighed 21.4 per cent as much as the tops. Hence the ratio of roots to tops in the case of brome grass was about 1:5, while in wheat and peas the roots showed a ratio of root to top by weight of about 1:30. In other words, brome grass had about six times as much root in comparison to the top as the other two species.

From these figures it would seem that the determination of the water requirement of the plant, on the basis of the dry weight of the aerial growth, is not necessarily an index to the ability of the plant to grow successfully in dry situations. To determine the moisture-absorbing power of a species account must also be taken of the depth and spread of the root system, as the volume of soil through which the roots penetrate is of the utmost importance in determining not only the amount of water available to the plant but the amount required by the tops. A plant may have a high water requirement when it is calculated on the basis of the weight of the tops, but at the same time it may be possessed of a root system great enough to supply the water necessary to the tops through its increased power to absorb. When the total water transpired by the plant is charged to the dry weight of the plant as a whole—that is, both aerial and subterranean parts—the water requirement data per unit of dry matter are quite different from those calculated on the aerial basis, as is shown in figure 3.

Since two factors, (1) water requirement, or expenditure, and (2) water gathering, or accumulation, are involved in the development of vegetation, further investigations may prove that the determination

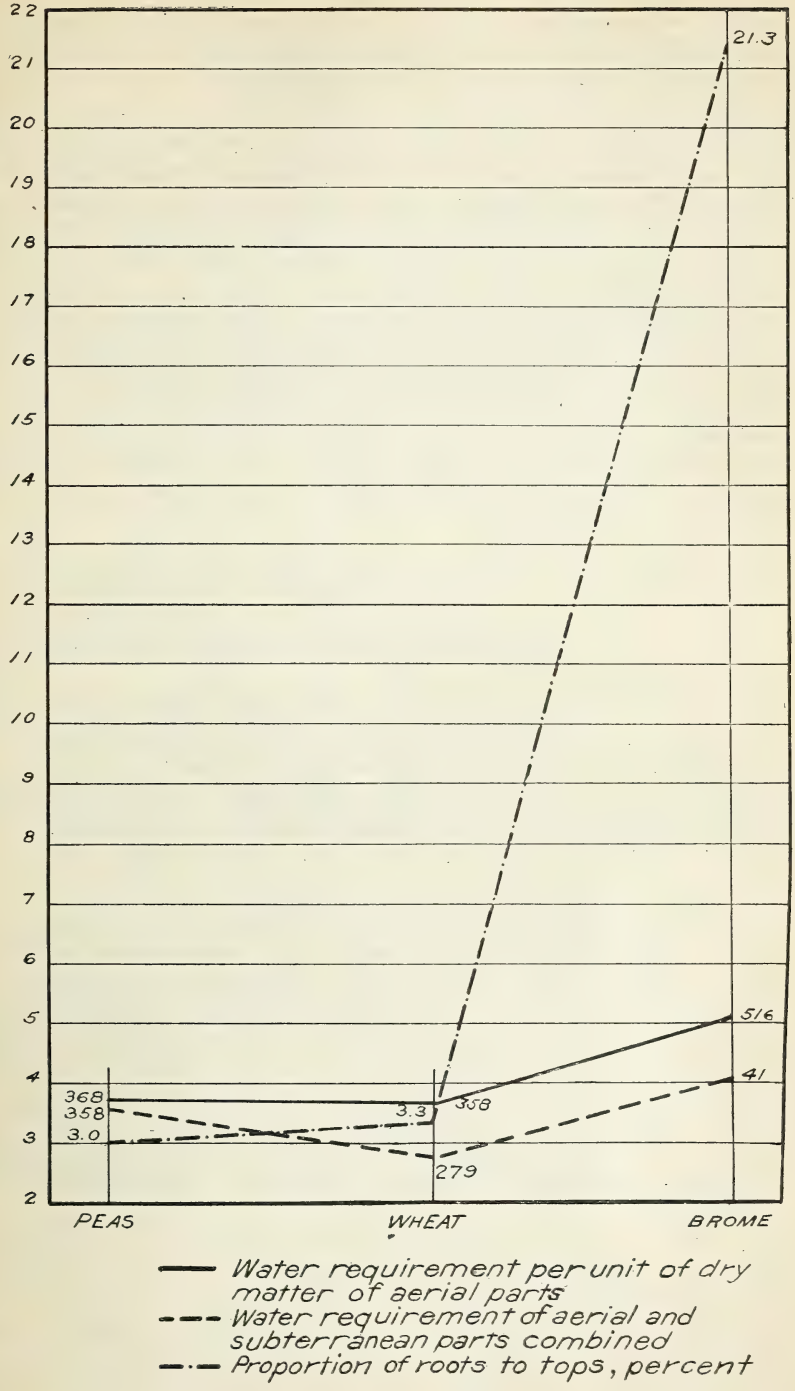


FIG. 3.—Water requirement of aerial and subterranean parts of peas, wheat, and brome grass, compared with the ratio of roots to aerial portion.

of water requirement on the basis of the plant as a whole may afford a more reliable index of successful growth in relation to drought than taking into account only the aerial portion of the plant. Most of the work on water requirement has been done in connection with cultivated plants, the root systems of which are small as compared with certain native species which may be classed as conservative users of water. The more dissimilar the root systems of species compared the less reliable the water requirement data will be unless the roots as well as the tops are taken into account.

The appreciably greater amount of water used by the plants grown in the fertile soil over those grown in the infertile soil is accounted for by the fact that the plants grew much more luxuriantly in the richer soil; hence the transpiration was much greater, and at the end of the season much more dry matter had been produced on the fertile than on the infertile soil. Exact data as to the vegetative development and the total water requirements of the species grown in the two soils are shown in Table 3.

TABLE 3.—*Summary of vegetative growth and water requirements of peas, brome grass, and wheat.*

| Data determined. | Peas. | | Native brome grass. | | Wheat. | |
|---|---|---|---|---|---|---|
| | Infertile soil. | Fertile soil. | Infertile soil. | Fertile soil. | Infertile soil. | Fertile soil. |
| Number of leaves | 42 | 112 | 35 | 84 | 22 | 47 |
| Leaf length (mm.) | 791 | 2,634 | 2,902 | 5,218 | 4,474 | 10,080 |
| Dry weight (grams) | 0.79 | 6.55 | 0.41 | 0.85 | 5.52 | 12.09 |
| Water used per plant (grams) | 667 | 3,051 | 553 | 944 | 2,516 | 3,820 |
| Water requirement per unit dry matter (grams) | 841 | 467 | 1,367 | 1,110 | 472 | 343 |

The graphical representation (fig. 4) of Table 3 shows remarkable contrast in the vegetative growth and total water requirement of the plants developed in the two soils. The number of leaves produced by field peas, for example, in the infertile soil as compared with that of the fertile soil is as 1 to 2.7; the leaf length, 1 to 3.3; the total dry weight produced, 1 to 8.3; and the water used per plant, 1 to 4.6. Similar contrasts are shown in the case of the other two species. The ratio in the water requirement per unit of dry matter, on the other hand, is reversed in the case of each species, as has previously been shown.

The above data show clearly the importance of exercising the greatest care in the selection and subsequent treatment of soils for the study of comparative growth of standard plants as a means of integrating climate. While soils obtained within a limited space and at the same depth, and having uniform appearance in color, texture, and other essentials, may be similar in many respects, they

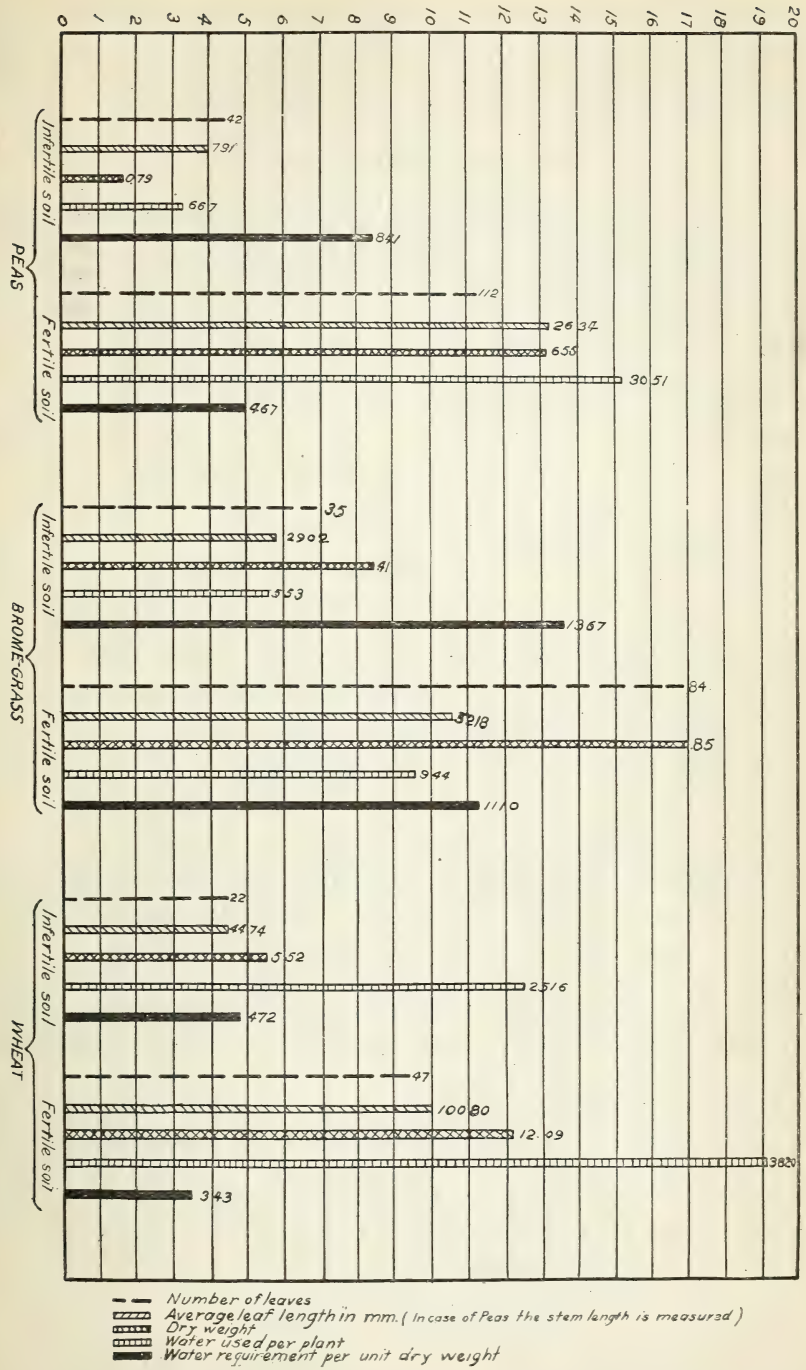


FIG. 4.—Summary of vegetative growth and water requirement of peas, native brome grass, and wheat in infertile and in fertile soils.

may differ appreciably in their crop-producing potentialities. Thorough mixing of the soil, therefore, regardless of the care with which it has been selected, can not be overemphasized as a means of avoiding outstanding errors from this source in experimentation.

## MEASUREMENT OF PLANTS.

At each of the type stations measurements of growth were made on the following number of specimens: 20 of wheat, 10 of peas, and 5 of native brome grass. The lid of each potometer contained five evenly spaced perforations (fig. 1). In the case of wheat, 10 seedlings were planted in each pot, 2 in each perforation; while in the case of peas and brome grass, each pot contained only 5 plants.

Throughout the growing season both leaves and stems of the plants were measured at regular intervals. The object of the measurements was to obtain data as to the relation of the environment to (1) the tendency of the plants to elongate their stems and (2) the tendency of the plants to expand their leaves. Measurements of the stems furnished direct data as to the rate of elongation of the plants. In obtaining leaf expansion, however, indices had to be used instead of actual figures on leaf area. Hence in the case of the grasses the leaf expansion was obtained by recording the length of the leaves; for, as will be shown in the calculation of the experimental error, leaf length is proportional to leaf area. In the case of the peas, an index of leaf area was obtained by recording the number of leaflets, as they were found to be of rather constant average size and were considered as units of area.

Since the seedlings were all of uniform size and inconsiderable in comparison to the subsequent growth of the plant, the measurements were considered as beginning at zero. During the first half of the growing season all the plants were measured at 10-day intervals. Owing to the number of plants grown and their luxuriant development, it became impossible in the first week in August to remeasure all of the plants at 10-day intervals; so from then on the measurements were made once a month.

At the end of the growing season in each type the plants were cut at the junction of the stem and the lid of the potometer, and the measurement again recorded. In addition, the dry weight and the ash content were determined. In the case of plants grown in the aspen-fir association, the soil was washed away from the roots and the dry weight of the latter obtained.

## EXPERIMENTAL ERROR.

In determining the rates of growth and other physiological activities for a given species some variations are sure to be found in indi-

vidual specimens or in plants grown in a single battery. These variations may be due to such features as slight differences in the fertility of the soil, but mainly they are accounted for by the natural tendency of individual plants to vary. In order to eliminate such individual variations, it is necessary to average the results secured from a large number of plants. In the present experiment the number of plants was sufficiently large to render the probable error of the average measurements of any battery at a given station much less than the difference in measurements between the plants of this battery and those of the corresponding batteries of the other stations. This fact is brought out in Table 4.

TABLE 4.—*Comparison between average error of the plant measurements at a given type station and the difference in experimental results of the respective type stations.*[1]

| Plant. | Type station. | Plant measurements. | Error in average. | Per cent average error. | Difference between measurements at type stations. |
|---|---|---|---|---|---|
| | | *Mm.* | *Mm.* | | *Mm.* |
| Brome grass [2] | Oak-brush | 12,569 | 1,358 | 10.80 | ..... |
| | Aspen-fir | 19,103 | 2,708 | 14.12 | 6,534 |
| | Spruce-fir | 5,064 | 818 | 16.13 | 14,039 |
| Wheat [2] | Oak-brush | 2,420 | 141 | 5.82 | ..... |
| | Aspen-fir | 4,296 | 290 | 6.75 | 1,876 |
| | Spruce-fir | 3,359 | 136 | 4.04 | 937 |
| Peas [3] | Oak-brush | 155 | 6 | 3.85 | ..... |
| | Aspen-fir | 127 | 4 | 3.10 | 28 |
| | Spruce-fir | 57 | 2 | 3.50 | 70 |

[1] The formula used in Tables 4 and 5 in deriving the *average error of the mean* is: the summation of all the variations from the mean, regardless of sign, divided by the number of cases times the square root of the number of cases.
[2] Average leaf length per plant.
[3] Average stem length per plant.

Table 4 shows the average leaf length (which is taken to represent leaf area) of typical specimens of mountain brome grass and wheat, and the average stem length of specimens of field peas grown in the respective type stations. From these data are computed the variations from the mean, the percentage of average error, and the difference between the measurements obtained at the type stations.

The greatest experimental error occurs in the case of mountain brome grass. This is accounted for by the fact that only 5 specimens of brome grass were grown in each type station, while in the case of the peas and wheat 10 and 20 specimens, respectively, were grown at each station. In each instance, however, the experimental error due to individual variation within a type is much less than the difference between two groups of different types.

Another source of error is the use of indices of leaf area instead of actual leaf area. Thus when the total length of the leaves of a wheat plant is used for comparative purposes, it is assumed that the total leaf length is proportional to the total area of the plant. The leaves of grasses are approximately triangular in shape, and their actual area may therefore be determined by multiplying the length of the leaf by the width and taking half of the product thus obtained. In order to ascertain whether the leaf length was a reliable index of leaf area, the leaf area was obtained in the manner described above for a number of cases and the results decided by the corresponding leaf lengths. Table 5 gives the leaf length, calculated area, the ratio of these two, the average error in millimeters, and the per cent determined by means of the formula given in the footnote to Table 4.

TABLE 5.—*Relation between leaf area and leaf length in wheat and mountain brome grass.*

| Specimen. | Total leaf length. | Total leaf area. | Leaf area. / Leaf length. | Variation from mean. | Per cent variation from mean. |
|---|---|---|---|---|---|
| Wheat: | *Mm.* | *Sq. mm.* | | *Mm.* | |
| 1 | 1,386 | 3,298.00 | 2.3795 | 0.0690 | 2.8 |
| 2 | 1,147 | 2,806.25 | 2.4465 | .0020 | .8 |
| 3 | 1,127 | 2,526.25 | 2.2415 | .2070 | 8.4 |
| 4 | 1,590 | 3,970.75 | 2.4973 | .0488 | 1.96 |
| 5 | 1,374 | 3,679.25 | 2.6777 | .2292 | 9.41 |
| Total | 6,624 | 16,280.50 | 12.2425 | .5560 | |
| Mean | | | 2.4485 | .0500 | 2.45 |
| Brome grass: | | | | | |
| 1 | 1,771 | 4,766.50 | 2.6910 | .2570 | 8.71 |
| 2 | 1,279 | 3,334.00 | 2.6060 | .3420 | 11.2 |
| 3 | 1,686 | 5,397.50 | 3.1820 | .2340 | 8.61 |
| 4 | 571 | 1,837.25 | 3.2170 | .2690 | 9.13 |
| 5 | 1,440 | 4,389.00 | 3.0470 | .0990 | 3.35 |
| Total | 6,757 | 19,724.25 | 14.7430 | 1.1930 | |
| Mean | | | 2.9480 | .1070 | 3.63 |

The fact that the ratio of leaf area to leaf length is nearly constant shows that the length furnishes a reliable index of area. The average error of the ratio for wheat, using 5 plants with about 25 leaves in all, is 2½ per cent; while in the brome grass, using 5 plants with about the same number of leaves as the wheat, the error is about 3½ per cent.

## MEASUREMENT OF PHYSICAL FACTORS.

Each of the three type stations was equipped, in the main, with automatic instruments. Air temperature, precipitation, evaporation, relative humidity, sunshine, and barometric pressure were recorded continuously at each station. In addition, a continuous record of the

wind movement was obtained at the two upper stations. The readings of all instruments were recorded daily at 8.30 a. m. and 4.30 p. m.

Because of the fact that certain important weather factors may be measured by various instruments, it is possible to get a number of different sets of values for the climatic factor, depending on the kind of instrument used. Where it is desired to compare physiological activities of plants with weather factors for short intervals, such as a few days, a single day, or a fractional part thereof, the kind of

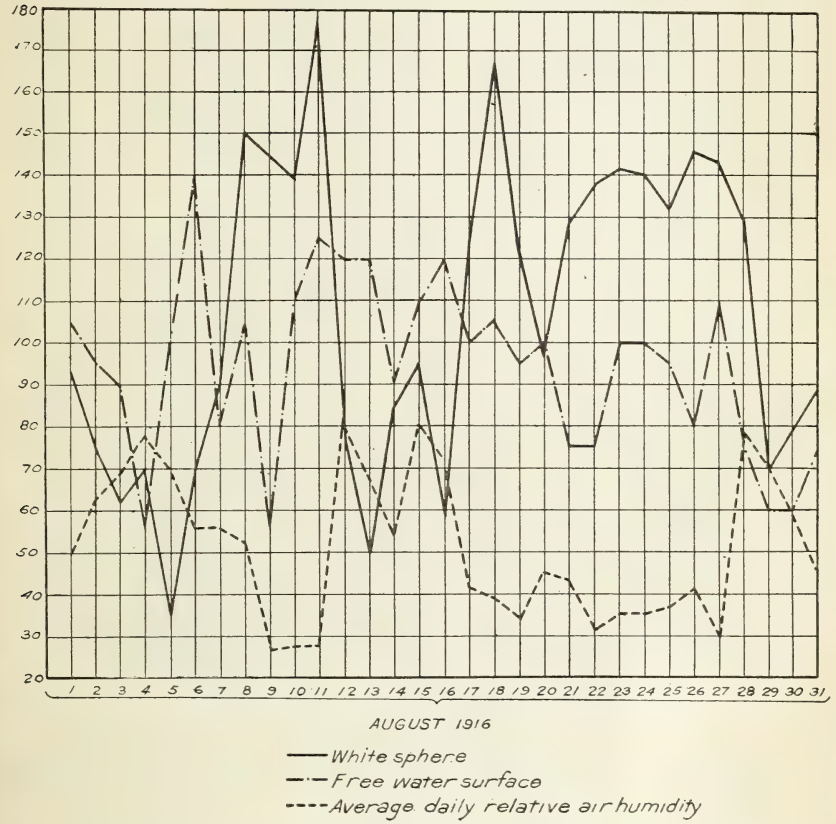


FIG. 5.—Evaporation from white sphere and from free water surface compared with average daily relative air humidity.

instrument used is often a matter of important consideration. The bearing which the choice of instruments has on the results obtained from the measurement of two of the climatic factors, evaporation and sunshine, is described in detail on pp. 18–24.

### AIR TEMPERATURE.

The temperature was measured automatically by carefully adjusted thermographs calibrated with standardized maximum and minimum

mercury thermometers and exposed in shelters of the Weather Bureau pattern 4½ feet from the ground.

### PRECIPITATION.

The precipitation record was obtained by means of automatic tipping bucket rain gauges, the data from which were harmonized

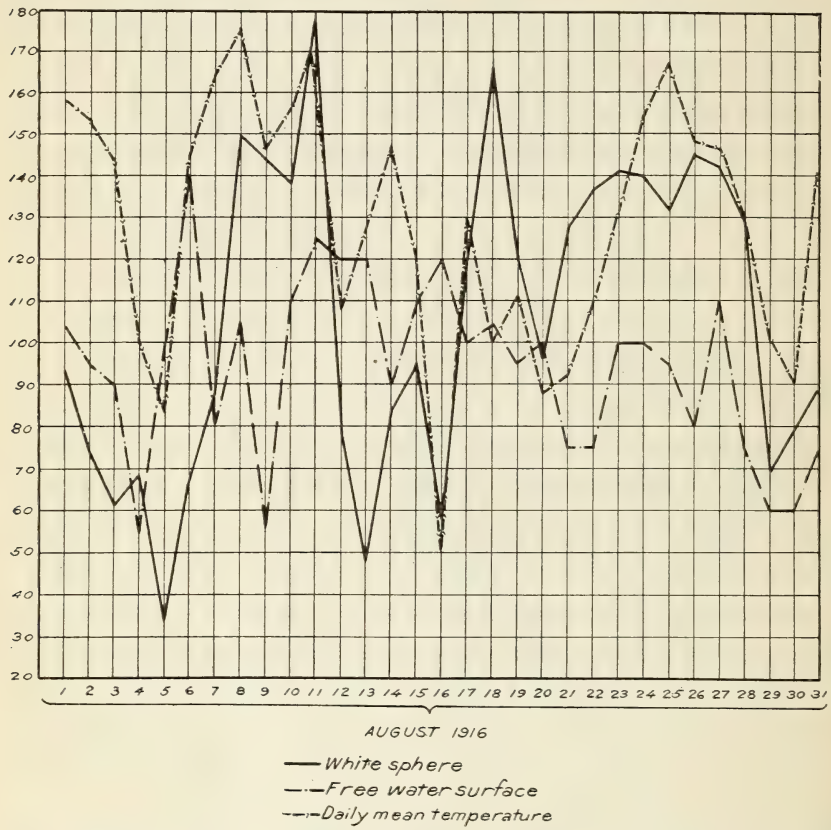


FIG. 6.—Evaporation from white sphere and from free water surface compared with daily mean temperature.

with standard rain gauges. In this way reliable data were obtained as to the amount and rapidity of the rainfall.

### EVAPORATION.

The evaporation was recorded in two ways: (1) By means of the standardized porous cylindrical and spherical atmometers, and (2) by means of a free water surface.

In the case of the porous spheres, both the black or radio cup and the white cup were used at each station. The spherical, as well as the white cylinder cups, were fitted with rain-correcting apparatus and

the mountings were self-contained as devised by Shive.[1] Distilled water was used, but in order further to insure accurate and comparable readings, the spheres, after a month of exposure, were replaced by restandardized spheres.

In measuring the evaporation from a free water surface a galvanized-iron evaporating pan, 10 by 36 inches, of the Weather Bureau pattern, was used. The evaporation from this free water surface

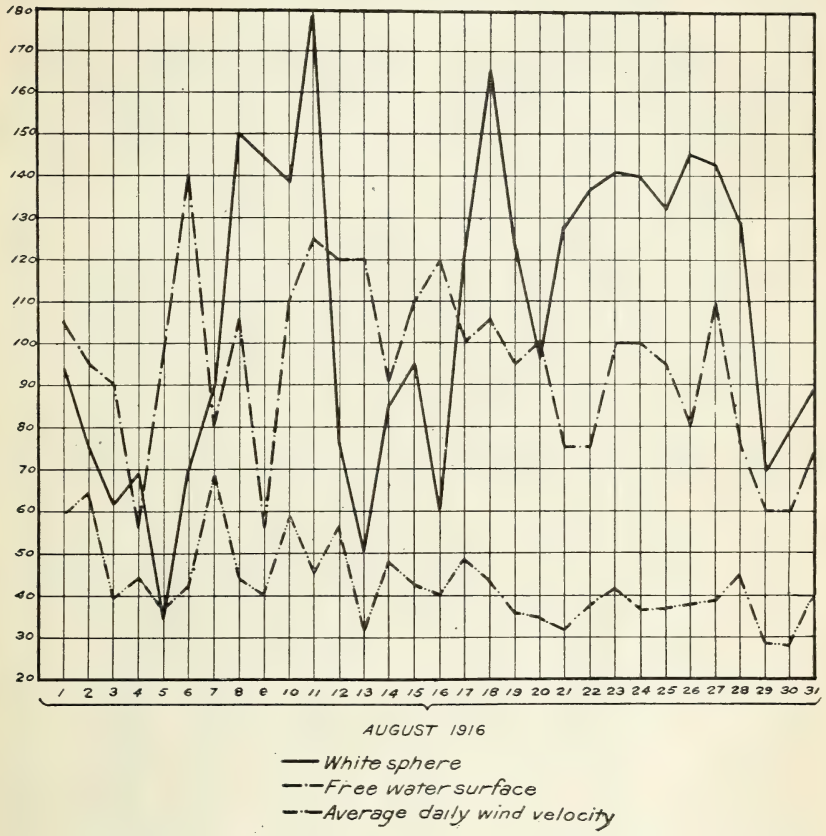


FIG. 7.—Evaporation from white sphere and from free water surface compared with average daily wind velocity.

was recorded by means of a hook gauge, reading in hundredths of an inch.

In order that the evaporation records obtained from the two types of instruments used might be compared directly, the porous spheres and the free water surface were placed at the same height, namely, 2½ feet above the ground.

[1] Shive, John W., An improved nonabsorbing porous cup atmometer. Plant World, vol. 18, No. 2 : 7–10. 1915.

Probably the variations in the measurements made with different instruments are greater in the case of evaporation than in the case of any other factor. Because of the lack of information as to the accuracy of certain available instruments in the measurement of evaporation, two different sets—the free water surface pan of the Weather Bureau pattern and the porous cup atmometer—were used in obtaining evaporation indices for comparison with plant activities, and it will be helpful in future field studies to compare the results.

As it was desirable to correlate evaporation and physiological activities for short periods, the evaporation values obtained from the readings of the spherical atmometer were first compared with those obtained from the free water surface and the data from each were then compared with the factors which chiefly determine the evaporation rate, namely, air humidity, wind movement, and air temperature. By this means it should be possible to show which of the two instruments is responding best to the conditions controlling evaporation. The records as obtained in the aspen-fir type for August were selected for this purpose. The data are presented in Table 6, and as a matter of convenience in comparing, they are summarized graphically in figures 5, 6, and 7.

TABLE 6.—*Daily evaporation from spherical atmometer and from free water surface, with corresponding relative humidity, temperature, and wind velocity.*

| Date. | Spherical atmometer. | Free water surface. | Average daily relative humidity. | Daily mean temperature. | Average daily wind velocity. |
|---|---|---|---|---|---|
| 1916. | *cc.* | *Inches.* | *Per cent.* | ° *F.* | |
| Aug. 1 | 18.8 | 0.21 | 50 | 65.9 | 5.9 |
| 2 | 15.0 | .19 | 63 | 65.6 | 6.5 |
| 3 | 12.1 | .18 | 69 | 64.4 | 3.9 |
| 4 | 13.6 | .11 | 78 | 60.1 | 4.4 |
| 5 | 6.8 | .20 | 70 | 58.4 | 3.7 |
| 6 | 15.3 | .28 | 56 | 64.4 | 4.2 |
| 7 | 17.8 | .16 | 56 | 66.4 | 6.9 |
| 8 | 29.9 | .21 | 53 | 67.6 | 4.4 |
| 9 | 28.8 | .11 | 27 | 64.6 | 4.0 |
| 10 | 27.5 | .22 | 28 | 65.6 | 5.9 |
| 11 | 36.7 | .25 | 28 | 67.1 | 4.6 |
| 12 | 15.3 | .24 | 81 | 60.8 | 5.6 |
| 13 | 9.8 | .24 | 67 | 62.7 | 3.1 |
| 14 | 17.0 | .18 | 54 | 64.6 | 4.9 |
| 15 | 18.9 | .22 | 81 | 62.1 | 4.3 |
| 16 | 11.6 | .24 | 72 | 55.0 | 4.0 |
| 17 | 24.5 | .20 | 42 | 63.2 | 4.9 |
| 18 | 33.2 | .21 | 40 | 60.0 | 4.4 |
| 19 | 24.2 | .19 | 35 | 61.1 | 3.6 |
| 20 | 19.2 | .20 | 46 | 58.8 | 3.5 |
| 21 | 25.5 | .15 | 44 | 59.2 | 3.2 |
| 22 | 27.4 | .15 | 32 | 60.8 | 3.8 |
| 23 | 28.2 | .20 | 36 | 63.0 | 4.2 |
| 24 | 27.9 | .20 | 36 | 65.4 | 3.7 |
| 25 | 26.4 | .19 | 37 | 66.7 | 3.7 |
| 26 | 28.9 | .16 | 42 | 64.8 | 3.8 |
| 27 | 28.5 | .22 | 30 | 64.6 | 3.9 |
| 28 | 25.7 | .15 | 79 | 63.1 | 4.5 |
| 29 | 13.8 | .12 | 69 | 60.1 | 2.9 |
| 30 | 16.0 | .12 | 59 | 59.0 | 2.8 |
| 31 | 17.7 | .15 | 45 | 64.3 | 4.1 |

The evaporation from the white spherical atmometer and the free water surface and the average daily relative humidity are shown in figure 5. In order to determine which of the evaporation curves is the most reliable for the periods under consideration, so far as relative humidity is concerned, note was taken of the number of cases in which the evaporation curves slope in a direction opposite to the corresponding humidity curve. As the relative humidity decreases, evaporation, other things being equal, would increase; hence it would be expected that the graph of instrumental evaporation values would show an opposite slope direction to the graph of relative humidity. For the graph representing the free water surface evaporation the slope is opposite on 19 days out of the 30, or in 63 per cent of the cases. The graph of evaporation from the spherical atmometer, on the other hand, slopes opposite to the relative humidity graph in 73 per cent of the total number of cases. In deriving these percentages, in the case of both evaporation graphs, it was deemed advisable to consider slopes as opposite in those cases in which they came very near being so, as well as when they were actually opposite. Since the evaporation curve for the spherical atmometer shows more cases of slope opposite to the relative humidity curve than does the evaporation curve for the free water surface, it may be considered that the atmometer is somewhat more reliable than the free water surface in determining evaporation for daily periods, in so far as evaporation is determined by relative humidity.

A comparison of the evaporation values obtained from the two instruments with the daily mean temperature is presented in figure 6. In this instance it would, of course, be expected that the evaporation curves would show agreement in slope with the curve representing the mean temperature. Examination of the graphs shows for the atmometer 67 per cent agreement (20 periods out of 30) with the temperature curve; and for the free water surface only 47 per cent (14 periods out of 30). If only slight disagreements between evaporation and temperature are considered, the per cent of agreement in the case of the atmometer record is even greater than that from the free water surface. It is interesting to note that the evaporation record obtained from the free water surface commonly lags about one day behind that of the temperature; that is to say, if the evaporation from the free water surface is compared with the temperature for the preceding period there is a much closer agreement than when the comparison is made for the same day. In order to obtain an evaporation record which is comparable with the transpiration of the plant for short periods, the instrument with which the evaporation is measured should respond quickly to temperature changes in a manner similar to the transpiration of the plant itself,

so that for this purpose the atmometer is superior to the free water surface.

Figure 7 shows the relation of evaporation, as obtained by the two methods, to wind movements. Here, again, agreement between the two graphs consists in a slope in the same direction, since high wind velocity accelerates evaporation rate and low wind velocity retards it. This figure shows an agreement of 11 periods in the case of evaporation from the free water surface with the average daily wind movement, or a percentage agreement of 37. The evaporation from the atmometer, on the other hand, shows for the same time an agreement of 18 periods, or a percentage agreement of 60.

From the above comparisons it is evident that the evaporation record obtained by means of the spherical atmometer agrees more closely with the relative humidity, the temperature, and the wind velocity, and is a more reliable index when short periods are to be considered than that obtained from the free water surface. When periods extending over several days or longer are considered, however, either instrument may be used with good results.

Because of the advantage of the rain-correcting device used in connection with the porous cup atmometer, this instrument was especially suited to the experiments here presented, and accordingly has been used throughout. Of the three types of porous cup atmometers available for field use, namely, the white sphere, the black sphere, and the white cylinder, all were operated in each type station throughout the season. The sum of the daily means of each set of cups and the difference in evaporation between the black and white sphere are presented in Table 7.

TABLE 7.—*Summary of evaporation from white cylindrical, white spherical, and black spherical atmometers, and of difference between white and black spherical atmometers during the period of experimentation.*

| Type. | White sphere. | Black sphere. | White cylinder. | Difference between black and white spheres. |
|---|---|---|---|---|
| | cc. | cc. | cc. | cc. |
| Oak-brush | 3,956.3 | 5,475.0 | 3,545.4 | 1,518.7 |
| Aspen-fir | 2780.3 | 4,025.4 | 2,490.8 | 1,245.1 |
| Spruce-fir | 4,251.3 | 5,530.2 | 3,711.7 | 1,278.9 |

The figures given in Table 7 are platted in figure 8. It is interesting to find that the graphs representing the three evaporating instruments here used are all practically parallel. This parallelism also holds for shorter periods, as is shown in figure 9. It would appear, therefore, that one might select any one of these instruments to ascertain the evaporation. However, because of the desire to use evap-

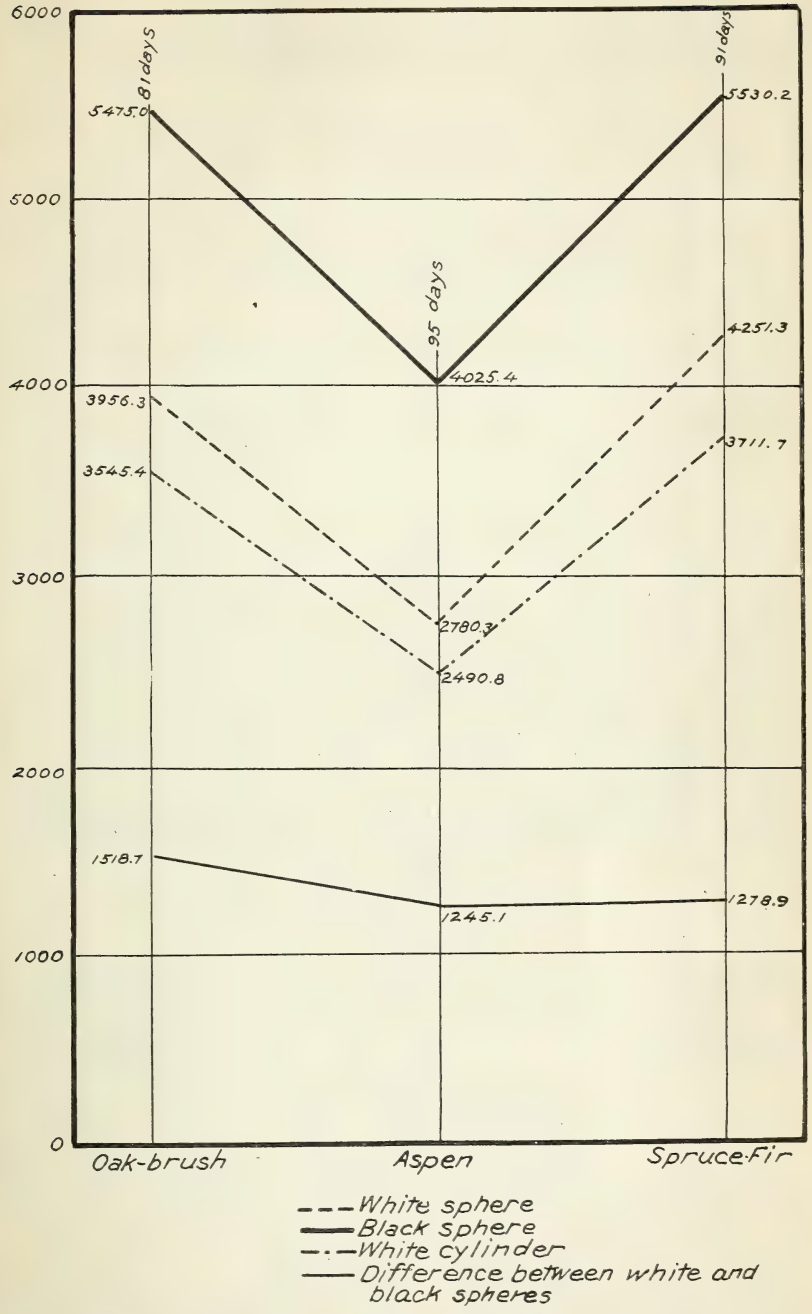


FIG. 8.—Summation of evaporation from white cylinder, white sphere, and black sphere and of differences between white and black spheres.

orating instruments which might also furnish data on sunshine intensity, the evaporation data from the white and black spherical atmometers have been used in connection with the plant studies.

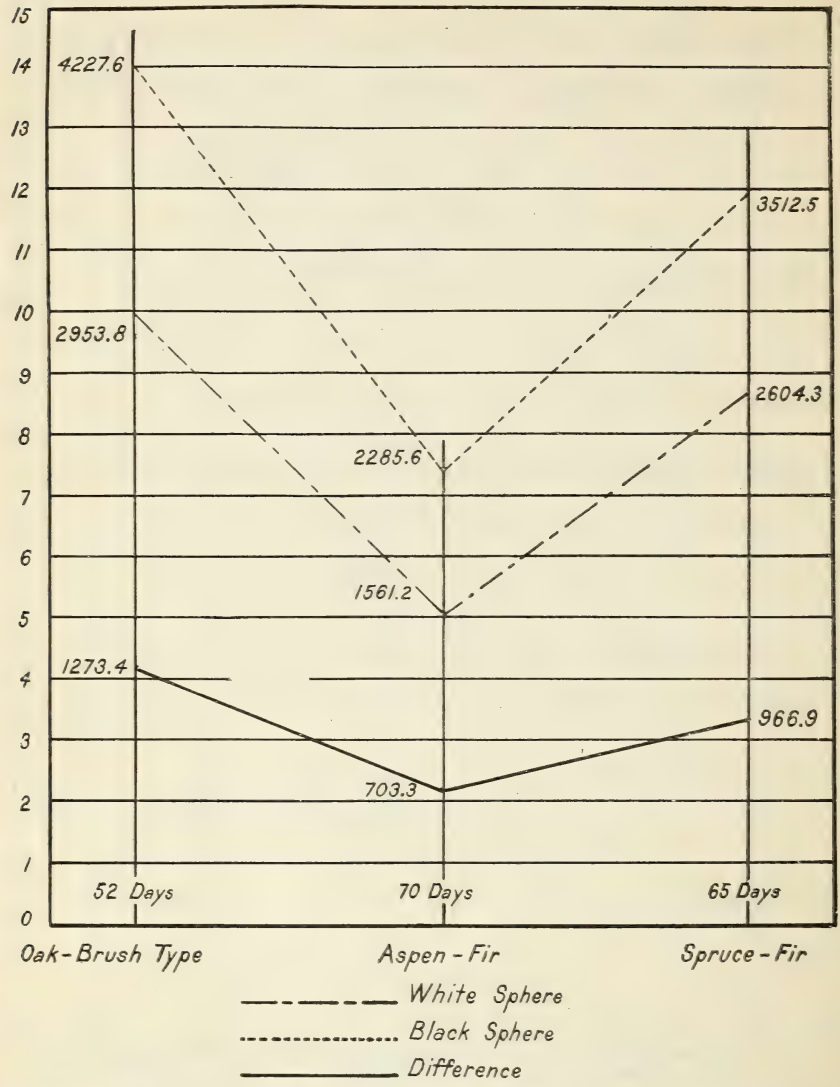


FIG. 9.—Summation of evaporation from black and white spheres and the difference between them. Record made during growth studies. Started late.

### BAROMETRIC PRESSURE.

The barometric pressure was measured by aneroid barometers. The instruments were standardized from time to time at the central station, where the elevation and pressure were known.

### WIND VELOCITY.

The wind velocity was measured automatically by anemometers of the Weather Bureau pattern located about 15 feet above the ground.

### SUNSHINE.

The records of sunshine obtained were for both duration and intensity.

The duration of sunshine was recorded automatically by means of the Marvin recorder used by the Weather Bureau.

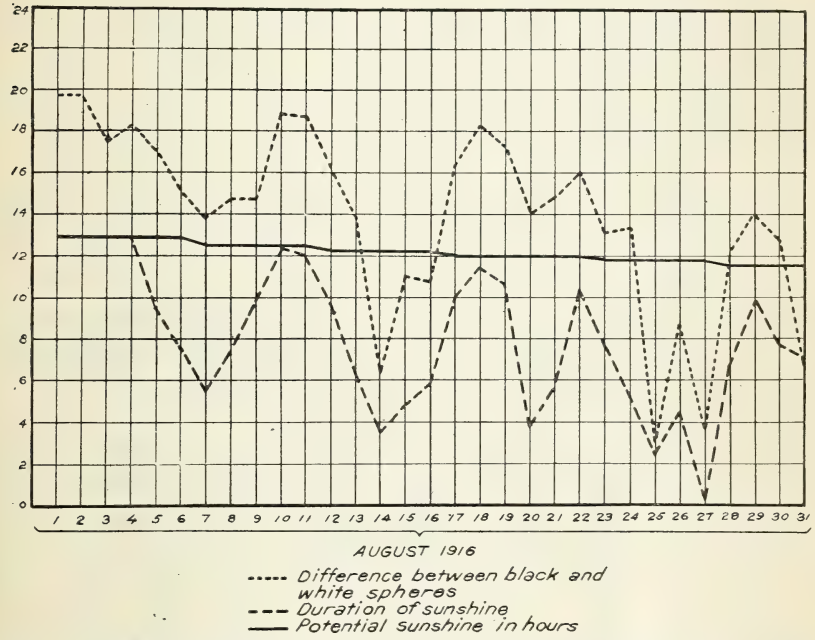


FIG. 10.—Difference between black and white spheres in evaporation as compared with hours of sunshine recorded by black bulb sunshine recorder.

Data on sunshine intensity were obtained by noting the difference in the evaporation between the radio-atmometer and the ordinary white porous cup atmometers.[1] The radio-atmometer used was a black sphere of the same size as the more common white form. Owing to its color it absorbs considerable of the radiant energy falling upon it, functioning in this regard much the same as foliage of ordinary plants. The white porous cup, on the other hand, absorbs comparatively little radiant energy and is therefore not appreciably affected by increased light intensity. Hence, while by night the

[1] Livingston, B. E. A radio-atmometer for comparing light intensity. Plant World, 14, No. 4: 96–99. 1911.

evaporation from the radio-atmometer and from the white porous atmometer of the same size and form is practically identical, by day the black cup, on account of its higher temperature, shows a greater rate of evaporation. Therefore the difference in the evaporation from the radio or black atmometer and the white atmometer affords a rough estimate of varying intensities of sunlight for the different periods and type stations. The actual variation intensity, of course, bears an important relation to transpiration and photosynthesis.

Only the duration of sunshine is measured by the Marvin sunshine instrument of the Weather Bureau pattern. Unless the investigator is working in the vicinity of an experiment station or similar base, the Marvin sunshine recorder can not, of course, be operated. The black and white porous cup atmometers, on the other hand, may be set up wherever desired. Accordingly, it is worth while to compare the sunshine records obtained from these two instruments. The data are given in Table 8 and are shown graphically in figure 10.

TABLE 8.—*Comparison of sunshine records obtained from a sunshine recorder of the Weather Bureau pattern, and the difference in evaporation between atmometers with black and white spheres. Readings taken in August, 1916.*

| Date. | Difference between black and white spheres. | Duration of sunshine (Marvin sunshine recorder). | Possible sunshine. | Date. | Difference between black and white spheres. | Duration of sunshine (Marvin sunshine recorder). | Possible sunshine. |
|---|---|---|---|---|---|---|---|
| 1916. | *cc.* | *Hours.* | *Hours.* | 1916. | *cc.* | *Hours.* | *Hours.* |
| Aug. 1 | 19.6 | 12.9 | 12.9 | Aug. 17 | 16.4 | 9.9 | 12.0 |
| 2 | 19.6 | 12.9 | 12.9 | 18 | 18.1 | 11.4 | 11.9 |
| 3 | 17.6 | 12.8 | 12.9 | 19 | 17.1 | 10.6 | 11.9 |
| 4 | 18.1 | 12.9 | 12.9 | 20 | 14.0 | 3.6 | 11.9 |
| 5 | 17.1 | 9.4 | 12.9 | 21 | 14.8 | 4.9 | 11.9 |
| 6 | 14.9 | 7.4 | 12.3 | 22 | 15.9 | 10.5 | 11.9 |
| 7 | 13.7 | 5.6 | 12.3 | 23 | 13.0 | 7.7 | 11.8 |
| 8 | 14.5 | 7.3 | 12.3 | 24 | 13.3 | 5.2 | 11.8 |
| 9 | 14.6 | 9.8 | 12.2 | 25 | 3.0 | 2.3 | 11.8 |
| 10 | 18.7 | 12.1 | 12.2 | 26 | 8.8 | 4.4 | 11.7 |
| 11 | 18.6 | 12.0 | 12.2 | 27 | 3.6 | 0.2 | 11.7 |
| 12 | 16.2 | 9.8 | 12.2 | 28 | 12.2 | 6.8 | 11.6 |
| 13 | 13.7 | 6.3 | 12.1 | 29 | 13.9 | 9.7 | 11.6 |
| 14 | 6.1 | 3.6 | 12.1 | 30 | 12.8 | 7.8 | 11.6 |
| 15 | 10.9 | 4.8 | 12.1 | 31 | 6.6 | 7.2 | 11.6 |
| 16 | 10.7 | 5.7 | 12.1 | | | | |

In following the slope of the curves as shown in figure 10, an agreement of 67 per cent (20 periods out of 30) is found, and the disagreements in practically all cases are relatively slight. The most conspicuous differences in ordinate values occur for days when the sky is partly cloudy and the sunshine more or less intermittent. In such instances there is almost invariably a much greater fluctuation in the values of the atmometric sunlight index than in the values of sunshine duration as recorded by the Marvin recorder. This may be accounted for by the fact that the evaporation from the black surface atmometer responds more quickly to fluctuation in sunshine than

does the mercury column of the sunshine recorder of the Weather Bureau type.

The data seem to warrant the statement that the use of atmometers in obtaining sunshine duration affords quite as reliable a record as does the more costly Marvin sunshine recorder. Of course, the impossibility of operating atmometers when the temperature drops below freezing makes them of value only during the growing season. Where it is desired merely to obtain a summary of the sunshine record, it is necessary to read the instruments only about twice per month, whereas the Marvin recorder must be read daily.

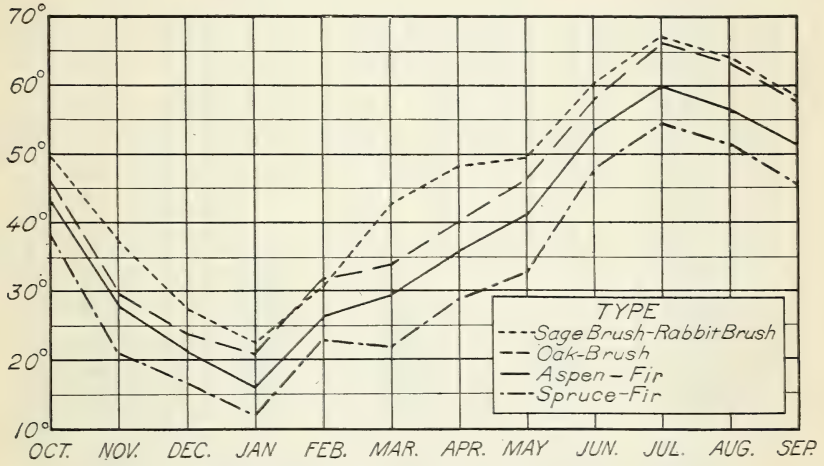


FIG. 11.—Monthly mean temperatures October, 1915–October, 1916.

## COMPARISON OF THE CLIMATIC CHARACTERISTICS OF THE THREE PLANT TYPES.

### TEMPERATURE.

For purposes of comparison there is probably no better way of showing differences in temperature in the type stations than to give the monthly mean temperature for each station. This is shown graphically in figure 11. Throughout the year the mean monthly temperature is appreciably lowest in the spruce-fir and highest in the sagebrush-rabbit-brush type. In general, the slopes of the mean-temperature curves of all the climatic types are similar, and this is especially true for the main growing season, from June to September, inclusive.

In the monthly range in temperature for the respective types there are even greater contrasts than in the daily means. The range in the monthly temperatures is shown in figure 12. These temperatures differ most notably from those given in figure 11, representing the monthly means, in (1) the similarity in vertical form and proximity

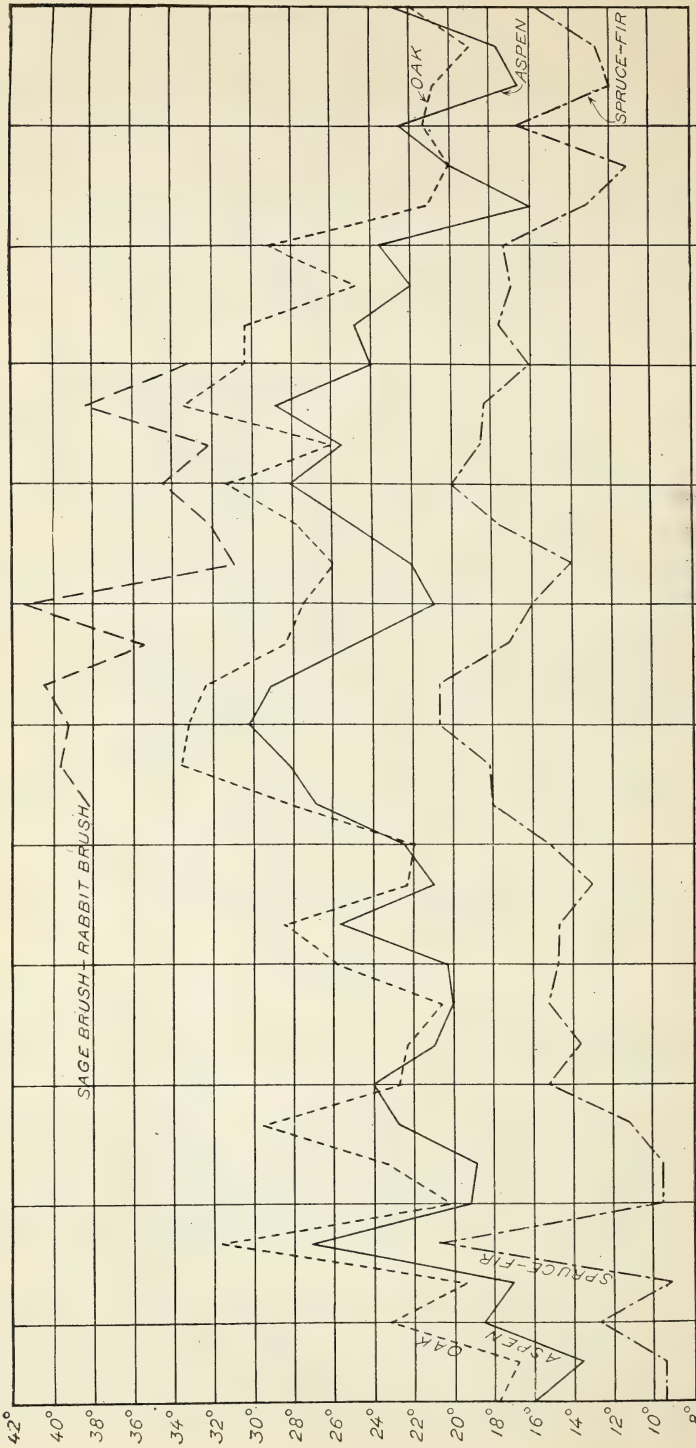


FIG. 12.—Range of temperatures in the four types January–December, 1916.

of the curves in the case of the oak-brush and the aspen-fir types, and (2) the decreased range or flattening of the curve in the spruce-fir type.

It is not possible by a review of the monthly mean temperatures to form a mental picture of the relative growing and nongrowing

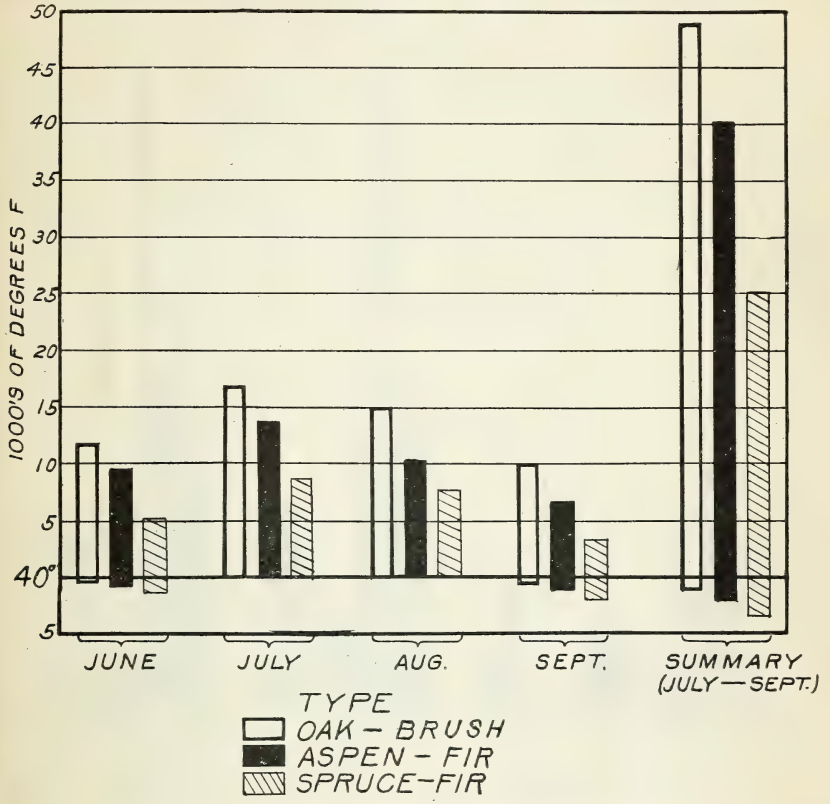


FIG. 13.—Summation of temperatures above and below 40° F., 1916.

temperatures; that is, the temperatures above or below 40° F. These are summarized in Table 9 and graphically represented in figure 13.

TABLE 9.—*Summary of temperatures above and below 40° F.*

| Month. | Temperature segregations. | Oak-brush type. | Aspen-fir type. | Spruce-fir type. |
|---|---|---|---|---|
| | | °F | °F. | °F. |
| June | above | 11,400 | 9,347 | 5,090 |
| | below | 350 | 767 | 1,399 |
| July | above | 16,919 | 13,773 | 8,843 |
| | below | 15 | 42 | 73 |
| August | above | 14,929 | 10,357 | 7,874 |
| | below | 0 | 74 | 103 |
| September | above | 10,222 | 6,838 | 3,505 |
| | below | 640 | 1,034 | 1,786 |
| Total | above | 53,470 | 40,315 | 25,312 |
| | below | 1,005 | 1,917 | 3,361 |

The smallest number of heat units above 40° F. and the largest number below 40° F., as shown in figure 4, occur in June and September, near the beginning and ending of growth in the two lower types represented.[1] One of the most significant facts brought out in Table 9 is the absence of temperatures below 40° F. for August,

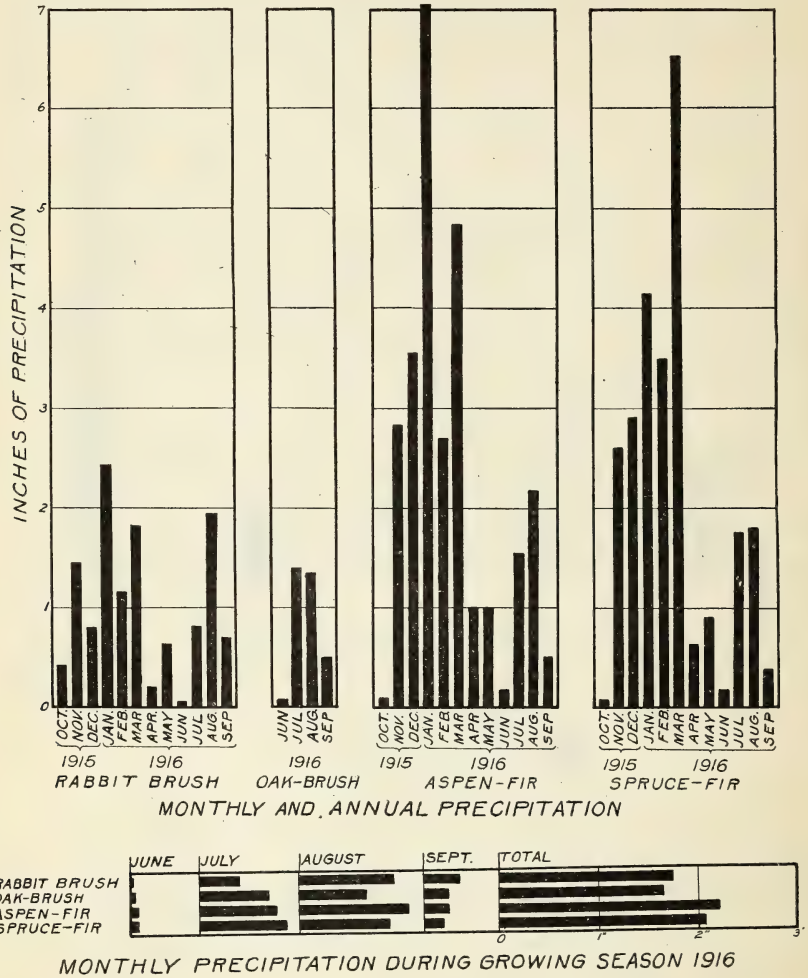


FIG. 14.—Precipitation record, 1915–1916.

in the oak-brush type. All types considered, July and August are the most favorable months for growth, in so far as it is determined by temperature.

[1] Growth begins in the oak-brush type approximately June 1. In the aspen-fir type the leaves begin to unfold about two weeks later. In the spruce-fir type growth begins between 3 and 4 weeks later than in the oak-brush type.

On the basis of the beginning of growth and the occurrence of killing frosts the growing periods in days for the respective types are approximately as follows:

| | |
|---|---|
| Oak-brush type | 120 |
| Aspen-fir type | 105 |
| Spruce-fir type | 70 |

### PRECIPITATION.

The monthly precipitation from October, 1915, to September, 1916, is summarized in figure 14.

In view of the higher temperature, the longer growing season, and the higher evaporation in the oak-brush type, it is significant that the annual precipitation is less in that type than in any of the more elevated types in which plant studies were conducted. The annual averages of precipitation of the types, including the untimbered type below the oak-brush, as recorded from 1914 to 1916, inclusive, are:

| | Inches. |
|---|---|
| Sagebrush-rabbit-brush type | 11.15 |
| Oak-brush type | 13.25 |
| Aspen-fir | 27.18 |
| Spruce-fir | 25.40 |

During the growing period in 1916 the aspen-fir type, as in the case of the three-year average, received the heaviest precipitation, nearly the same amount, however, being recorded in the type immediately above.

### EVAPORATION.

Monthly evaporation and precipitation are represented in the same figure (fig. 15). Owing to the occurrence of freezing temperatures in June, particularly in the two higher types, unbroken evaporation records were obtained only from July to September, inclusive.

Figure 15, based upon the records of the porous cup atmometer (see fig. 16), shows that the highest evaporation occurs each month in the oak-brush type. In the spruce-fir type the evaporation is nearly as great as in the lowest association, while in the aspen-fir type it is much less than in either of the others. Table 7 and figure 8 also indicate that the evaporation in the oak-brush and spruce-fir types is much greater than in the aspen-fir type.

In the case of growth studies begun in the stations at a later period, the summation of evaporation is quite as contrasted, as is shown in figure 9. While the records in this series of experiments cover a shorter period than those in the original study, being 52, 70, and 65 days in the oak-brush, aspen-fir, and spruce-fir types, respectively,

evaporation was notably greater in the lowest type, least in the central, and intermediate in the highest.

The high evaporation in the oak-brush type is due chiefly to high temperatures and low relative humidity. In the spruce-fir type the high evaporation is accounted for chiefly by the high wind velocity, as will be shown later. Owing to the aspen-fir type being intermediate in elevation between the other two, and having a notably heavier stand of vegetation, especially tree growth, the factors influencing evaporation are in no instance extreme.

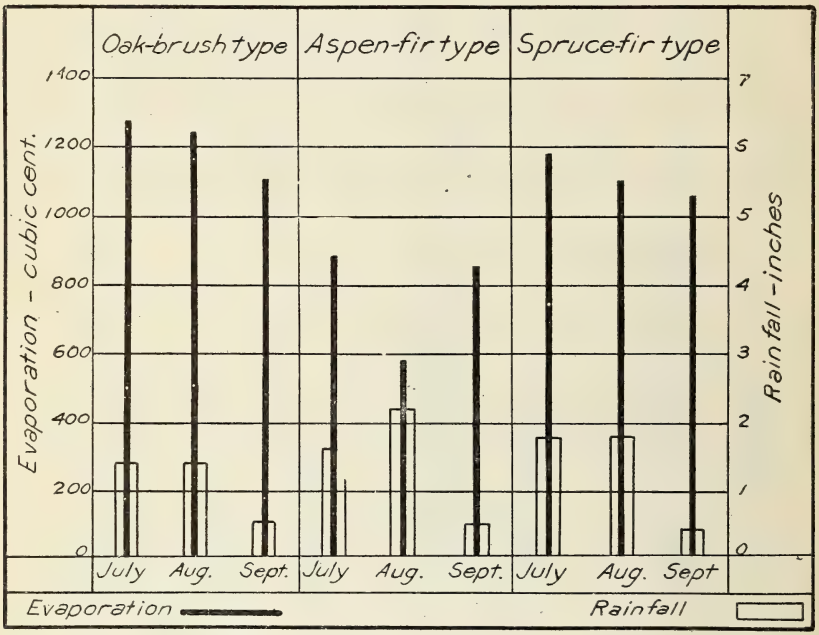


FIG. 15.—Monthly evaporation from spherical atmometers and corresponding precipitation in type stations, 1916.

### WIND VELOCITY.

Largely because of the physiographical features, the velocity of the wind is notably greater in the spruce-fir type than in the lower associations. The comparative intensity of this factor may be appreciated readily by summing the daily wind movement by monthly periods. Since the wind velocity during the growing season is probably an influential factor in the development of the vegetation, data are presented in Table 10 showing the wind movement during the growing seasons of 1915 and 1916.

TABLE 10.—*Monthly wind movement in the spruce-fir and in the aspen-fir type station.*

| Month. | Year. | Aspen-fir. | Spruce-fir. |
|---|---|---|---|
| | | *Miles.* | *Miles.* |
| June | 1915 | 3,081 | 6,501 |
| | 1916 | 3,020 | 7,119 |
| July | 1915 | 3,055 | 6,807 |
| | 1916 | 3,697 | 5,505 |
| August | 1915 | 3,339 | 4,836 |
| | 1916 | 3,198 | 5,116 |
| September | 1915 | 3,008 | 7,632 |
| | 1916 | 3,080 | 6,873 |
| Total | 1915 | 12,483 | 25,776 |
| | 1916 | 12,995 | 24,613 |

FIG. 16.—View of atmometers and evaporating pan used in measuring the evaporating power of the air.

The above figures show that the wind movement during the growing seasons of 1915 and 1916 was greater by approximately 100 per cent in the heart of the spruce-fir type than in the aspen-fir association 1,300 feet lower. In summarizing the wind movement by 10-day periods the velocity is found to exceed by 200 per cent that in the aspen-fir type for certain periods. Obviously, the gales over the elevated, sparsely vegetated plateaus have a profound effect on the evaporation and to some extent at least on the transpiration rate of the vegetation.

### SUNSHINE.

In recording the sunshine it was deemed advisable to note both the possible and the actual duration, since both are important to the development of vegetation. These factors are graphically shown in figure 17 for the aspen-fir type during the seasons of growth in 1915 and 1916.

In 1915 the greatest actual sunshine occurred in July, while in 1916 it was recorded in June. Owing partly to the advancement in the season but chiefly to the topographic features adjacent to the meteorological stations, there is a gradual decline in the potential sunshine duration throughout the growing season. The potential and actual sunshine durations, on the basis of three seasons' records,

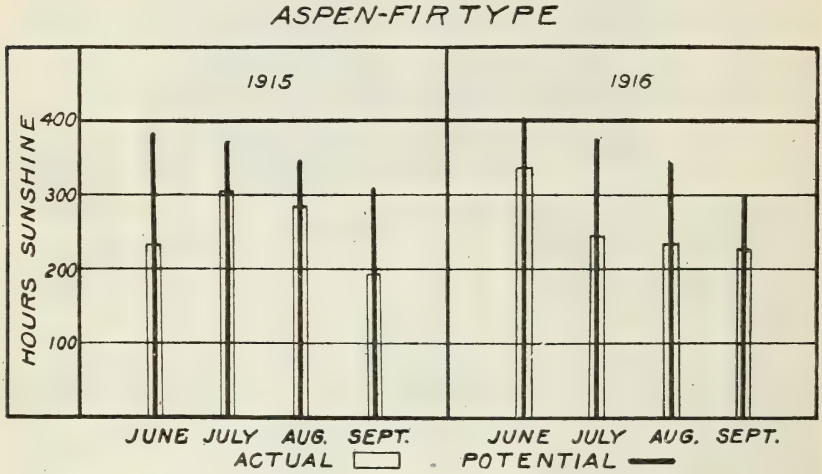


FIG. 17.—Actual and potential sunshine during growing season in the aspen-fir type, 1915.

are found to be practically identical in the three associations studied; consequently, no attempt is made to correlate sunshine duration with the plant activities.

### BAROMETRIC PRESSURE.

So far no direct fundamental relations have been established between barometric pressure and the development of the plant.[1]

The relation of high and low pressure to local rainstorms and high winds was observed in the aspen-fir association throughout the growing season of 1916, and the results are shown in figure 18.

Practically always when the pressure dropped appreciably below normal a change followed in the weather. While the amount of precipitation and the movement of the wind are not necessarily pro-

[1] Zon, Raphael, Meteorological observations in connection with botanical geography, agriculture, and forestry. Monthly Weather Review, April, 42: 217–23. 1914.

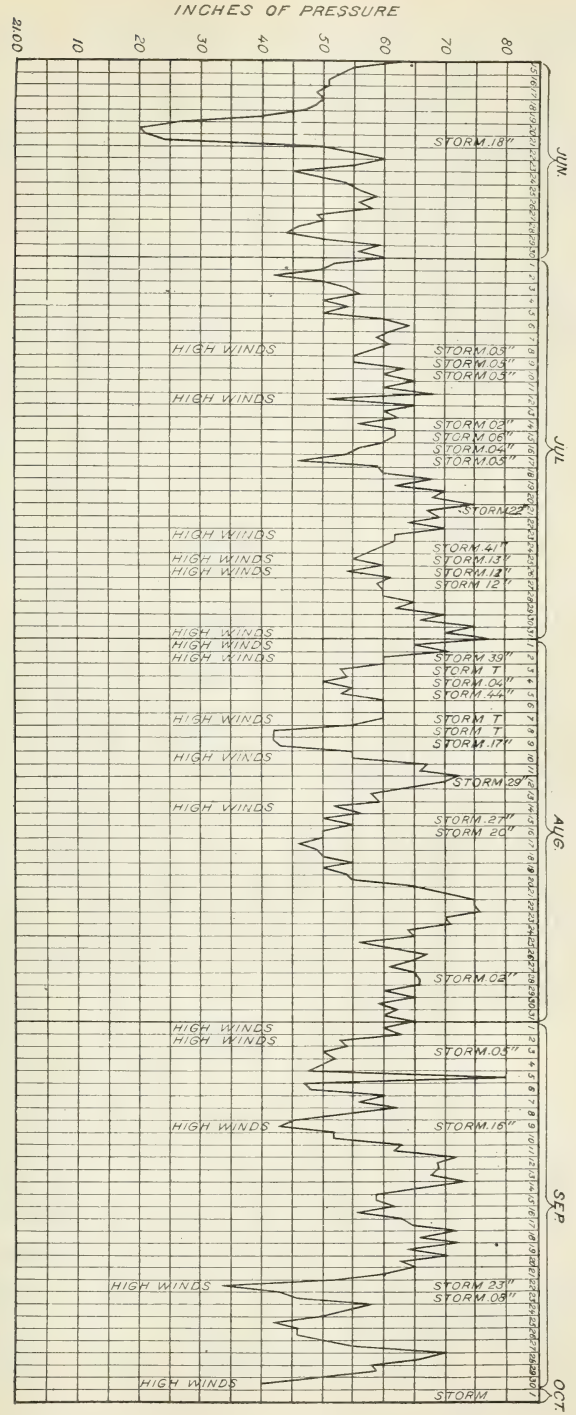


FIG. 18.—Barometric pressure and its relation to storms, 1916.

portional to the pressure below normal, figure 18 indicates that local observations of pressure are of some value in forecasting changes in the weather conditions where the daily weather map is not available. As stated, however, the relation of pressure to vegetative activities can best be expressed by the summation of certain other factors correlated with pressure and known to exert a direct influence on the development of the plant.

### SUMMARY OF CLIMATIC COMPARISONS.

The climatic characteristics of the plant-type zone may be summed up as follows: The mean annual temperature is highest in the least elevated type zone and decreases gradually with the increase in altitude until, in the spruce-fir association, the season of growth covers a period of only 70 days. In the oak-brush type zone the growing season is approximately 120 days. Precipitation, on the other hand, is normally only about half as heavy in the oak-brush type as in the type zones above. In general, however, the precipitation is somewhat heavier in the aspen-fir than in the spruce-fir type zone. The precipitation is rather uniformly distributed throughout the year. The evaporation is highest in the oak-brush type, where the greatest heat units and least rainfall are recorded. The evaporation factor is nearly as intensive in the spruce-fir type, however, while in the aspen-fir association it is only about half as great. The strong evaporation in the spruce-fir type is accounted for by the high wind velocity, which often exceeds 40 miles per hour for several hours in succession. The seasonal wind movement in the spruce-fir type is approximately 100 per cent greater than in the associations below. The possible and actual sunshine are found to be practically identical in the respective types. The barometric pressure, of course, varies with the elevation, but the seasonal fluctuations in a given locality are slight and insignificant so far as concerns any direct effect on the vegetation.

### TEMPERATURE SUMMATIONS.

Owing to the mass of climatic data compiled, it was necessary to simplify them by summarizing[1] on different bases.

The temperature factor in the respective stations for the periods during which the plants were under observation was summarized in three ways: (1) By physiological temperature coefficients as developed by Lehenbauer[2] and later applied by Livingston;[3] (2) the

[1] The literature relative to methods of comparative summations of climate has been reviewed by Abbe, Cleveland, First report on the relation between climate and crops. U. S. Weather Bureau Bull. 36, 1905.

[2] Lehenbauer, P. A. Growth of maize seedlings in relation to temperature. Physiol. Res. 1 : 247–288. 1914.

[3] Livingston, Burton E. Physiological temperature indices for the study of plant growth in relation to climatic conditions. Physiol. Res. 1 : 399–420. 1916.

sum of the positive or effective temperatures, that is, the sum of the means above 40° F., as originally proposed by Merriam,[1] and (3) the sum of the daily mean temperatures. For comparison with plant growth in this study, the sum of the temperature efficiencies for the growth periods has been used instead of the average temperature efficiency. This was done for the reason that the plant measurements represent total growth for the respective periods.

Physiological temperature coefficients are based upon data obtained by Lehenbauer in the study of the elongation of the shoots of maize sprouts when exposed to practically constant temperature for 12-hour periods. These 12-hour exposures were made degree by degree at temperatures ranging from the minimum at which growth takes place, through the optimum, and on to the maximum temperature at which growth is possible. Varying increments of elongation naturally took place according to the temperature to which the sprouts were exposed; and these growth rates were platted against the temperature used, giving a curve showing the relation between temperature and the rate of growth of the plant. The lengths of the ordinates of this growth curve furnish a series of numbers which represent the efficiency of the various temperatures in promoting the growth of maize. The application of the physiological temperature coefficient to any plant other than the one used by Lehenbauer is based on the assumption that the general relation of growth and temperature is the same as for the maize. Whether or not the physiological temperature indices obtained under controlled conditions will apply to field plants where the temperatures fluctuate widely can not be stated. It may be presumed for the present, however, that they will more closely account for physiological responses of field plants than will direct temperature summations.

Since these indices are based on physical and chemical processes taking place within the plant, temperatures at which no appreciable activities take place are at once eliminated; at the same time the efficiency of the temperature up and down the thermometer scale receives the proper weight.

In applying this method of temperature summation the daily mean temperatures were first obtained from the hourly corrected thermometer readings for the period during which the plants in the type stations were grown. The corresponding physiological indices were then substituted for the daily means and these indices summed for the period in question.

By positive or effective temperatures is meant the number of degrees of temperature above the minimum at which growth can take

[1] Merriam, C. Hart. Life zones and crop zones in the United States. U. S. Department of Agriculture Bull. 10: 55–73. 1898.

place. On the basis of many plants studied this minimum may be placed at approximately 40° F. Hence in the periodic and seasonal temperature summations, the daily mean temperature less 40, the uneffective growing temperature, were added. These summations of effective temperatures were made, in the case of each of the type stations, for the period *in toto* during which the plants were grown, as well as for shorter periods. This method involves a slight error, since in a few instances during the growing season the mean dropped below 40°; but the error thus introduced is so small as to be quite negligible.

The sum of the daily mean temperatures was obtained from the hourly corrected thermograph readings and added according to definite periods. These summations are presented chiefly for purposes of comparison with the other two methods of summation described.

The temperature summations by the three methods are given in Table 11, in Section A, of the table for the plants that were started June 13 and grown until killing frosts arrested their activities, and in Section B, for those started several weeks later and grown until inclement weather set in.

TABLE 11.—*Temperature summations, in degrees Fahrenheit, for period of growth of potometered plants in type stations.*

SECTION A.[1]

| Type. | Duration of period. | Sum of daily mean. | Sum of positive temperature. | Sum of physiological temperature efficiency. |
|---|---|---|---|---|
| | *Days.* | °*F.* | °*F.* | *Index.* |
| Oak-brush | 81 | 5,034 | 1,789 | 2,473.7 |
| Aspen-fir | 95 | 5,445 | 1,404 | 1,560.6 |
| Spruce-fir | 91 | 4,631 | 991 | 730.5 |
| SECTION B. | | | | |
| Oak-brush | 52 | 4,330 | 1,528 | 1,938.2 |
| Aspen-fir | 70 | 3,932 | 1,132 | 1,025.8 |
| Spruce-fir | 65 | 3,285 | 685 | 486.1 |

[1] Section A of the table has reference to fig. 19, and Section B to fig. 20.

It should be pointed out that the temperature summations in the case of the oak-brush type are for a period of 81 days, which marks approximately the time required for the maturity of the plants. The summations in the aspen-fir and spruce-fir associations are for 95 and 91 days, respectively. Owing to the relatively low temperatures the plants in the two latter types did not reach maturity, killing frosts having occurred early in September. From the temperature summations in figure 19, therefore, it should be understood that the

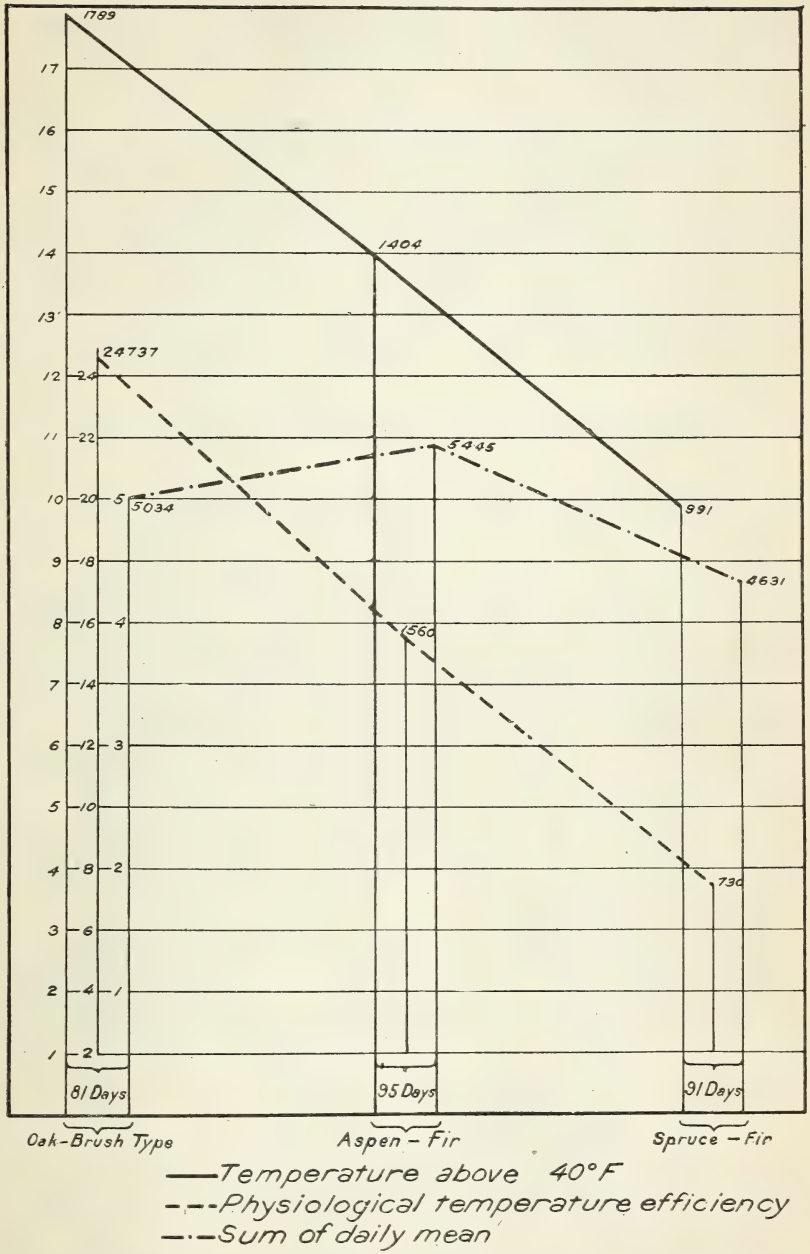


FIG. 19.—Temperature efficiency summations for period of growth of plants used in main experiment.

data given for each station represent slightly different numbers of days. In figure 19, as well as in certain other graphs, the curves are comparable in each case as to direction of slope; but it should be

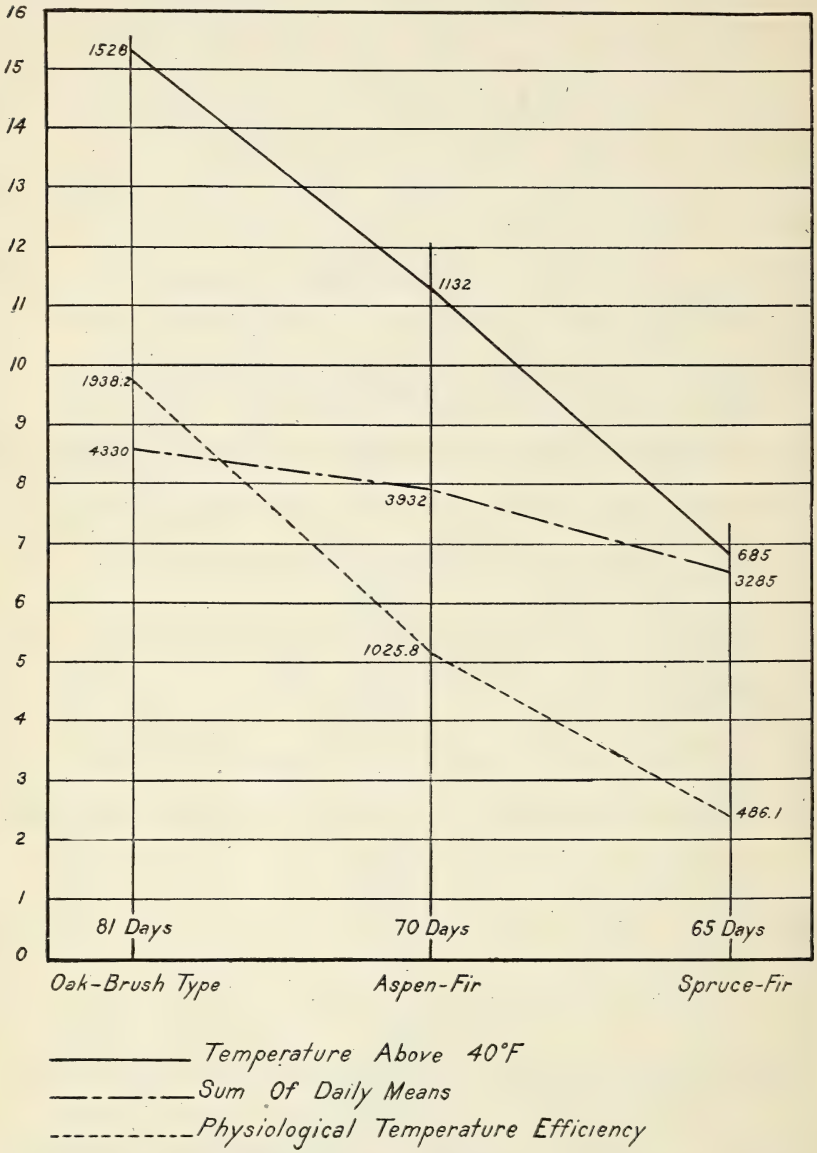


FIG. 20.—Temperature efficiency summations for period of growth of special experiments.

understood that the lengths of the ordinates are not in all cases directly comparable; the vertical scales employed are merely convenient ones and are quite arbitrary.

It is a noteworthy fact that the summed physiological temperature coefficients and the sum of the positive temperatures; that is, those above 40° F., bear practically the same relation to each other in the respective type stations. This has also been observed to hold true, in general, for shorter periods (fig. 20). Neither of these summations, however, agrees with the sum of the daily temperatures. As will be shown elsewhere, both the physiological temperature coefficients and the sum of the positive temperatures show some relation to growth and other plant activities. This does not appear to hold true of the summation of the daily mean temperature. Because of the corresponding slopes of the graph in figure 19 between the physiological temperature summation and the sum of the positive temperatures, either may be used for comparison with the plant-growth data in the case of the batteries observed for the period in question.

## CORRELATION BETWEEN GROWTH AND ENVIRONMENTAL FACTORS.

### RELATIVE DEVELOPMENT OF THE PLANTS IN THE TYPE STATIONS, AND THE CORRESPONDING WATER REQUIREMENTS.

A summation of the data obtained for the development and water requirements in the different type stations of wheat, peas, and brome grass (based on dry weight of tops) is given in Table 12. These figures represent the activities of the plants for 81 days in the oak-brush type, 95 days in the aspen-fir type, and 91 days in the spruce-fir type. The temperature indices and evaporation summaries for the respective periods are given in figures 19 and 8.

TABLE 12.—*Summation of growth and water requirements of plants developed in the type stations.*

| Type. | Plant. | Average stem height of peas and leaf length of wheat and brome grass. | Number of leaves. | Water requirement per unit dry matter. |
|---|---|---|---|---|
| | | *Mm.* | | *Grams.* |
| Oak-brush | Wheat | 3,990 | 28 | 626 |
| | Peas | 4,781 | 206 | 779 |
| | Brome grass | 15,980 | 125 | 803 |
| Aspen-fir | Wheat | 8,560 | 53 | 288 |
| | Peas | 11,863 | 398 | 368 |
| | Brome grass | 22,290 | 144 | 516 |
| Spruce-fir | Wheat | 5,280 | 26 | 300 |
| | Peas | 5,584 | 166 | 345 |
| | Brome grass | 8,114 | 81 | 756 |

The values given in Table 12 are platted in figures 21, 22, and 23. The most striking features brought out in the graphs are (1) the greater vegetative development, including number of leaves, leaf

length, and stem height, in the aspen-fir association, and (2) the relatively high water requirement for the production of a unit of dry matter in the oak-brush type.

In the case of peas, the number of leaves produced in the aspen-fir type, as compared with the oak-brush and spruce-fir types, respectively, is approximately in the ratio of 4, 2, and 1.7. The leaf length of wheat shows a ratio of about 2, 1, and 1.3 in favor of the aspen-fir

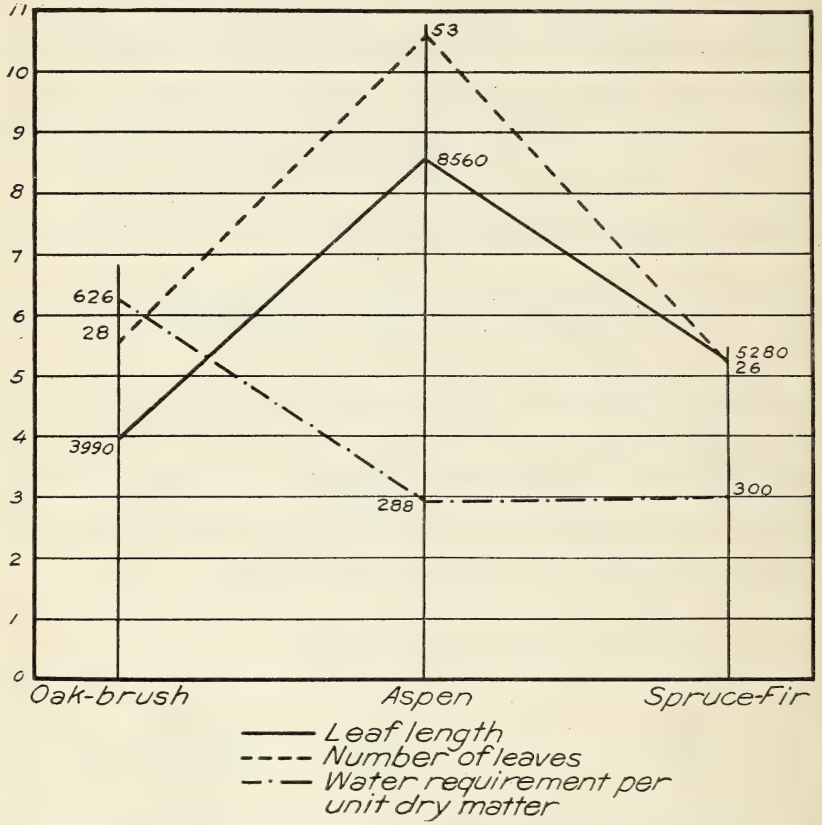


FIG. 21.—Water requirements and vegetative growth of wheat in the three climatic types.

association. In the case of the brome grass practically the same relations exist.

In each instance the water requirement per unit of dry matter is the highest in the oak-brush type. The fact that the plants were grown for a longer period in the highest and middle stations would naturally imply that they used more total water, but not necessarily that they had a higher water requirement per unit of dry weight. A comparison shows that in the case of wheat and peas the water requirements are very nearly the same in the central and in the

highest types, while brome grass shows a greater demand for water in the spruce-fir type than in the aspen-fir type. All three species exhibit a markedly interesting relation of development to water requirement, namely, that the lowest water requirement for the production of a unit of dry matter is invariably associated with the most luxuriant growth. Further, figure 8 shows that the evapora-

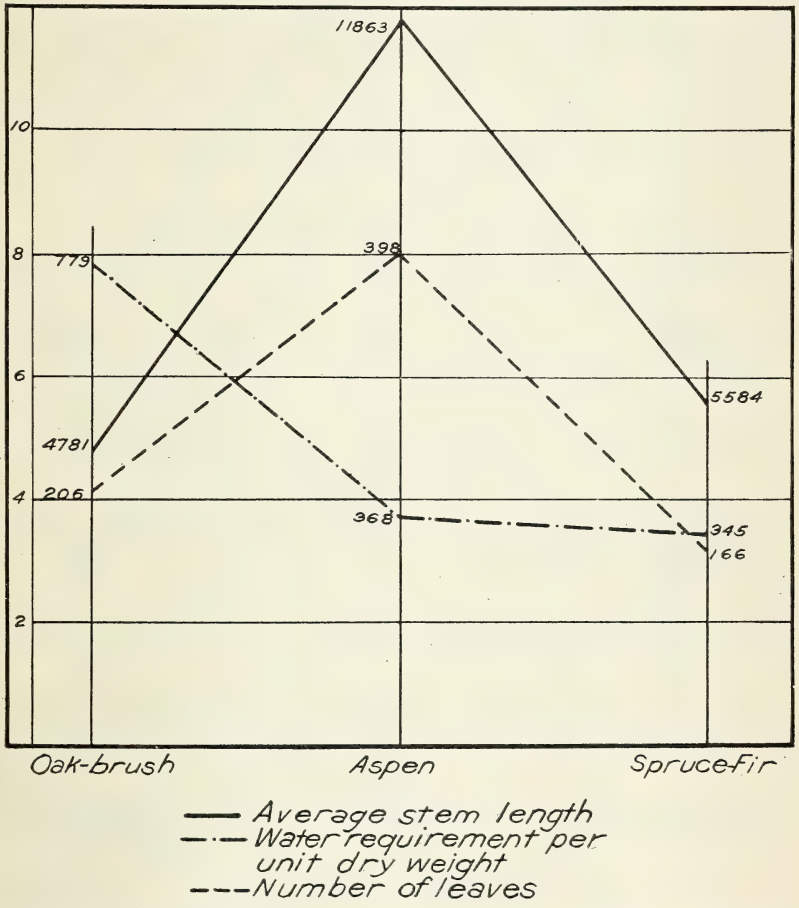


FIG. 22.—Water requirements and vegetative growth of Canada field peas in the three climatic types.

tion curve, corresponding to the period of growth of the plants, slants in the opposite direction from those of the development of the plants as platted in figures 21, 22, and 23. In the oak-brush type, where the water requirement is highest, evaporation is most intensive.

The data on the relative development of the plants in the type stations and the corresponding water requirements are especially important, since they represent vegetative activities throughout the

season. Hence these data appear to throw some light on the causes of failure or success of experimental trials with plants in the types represented.

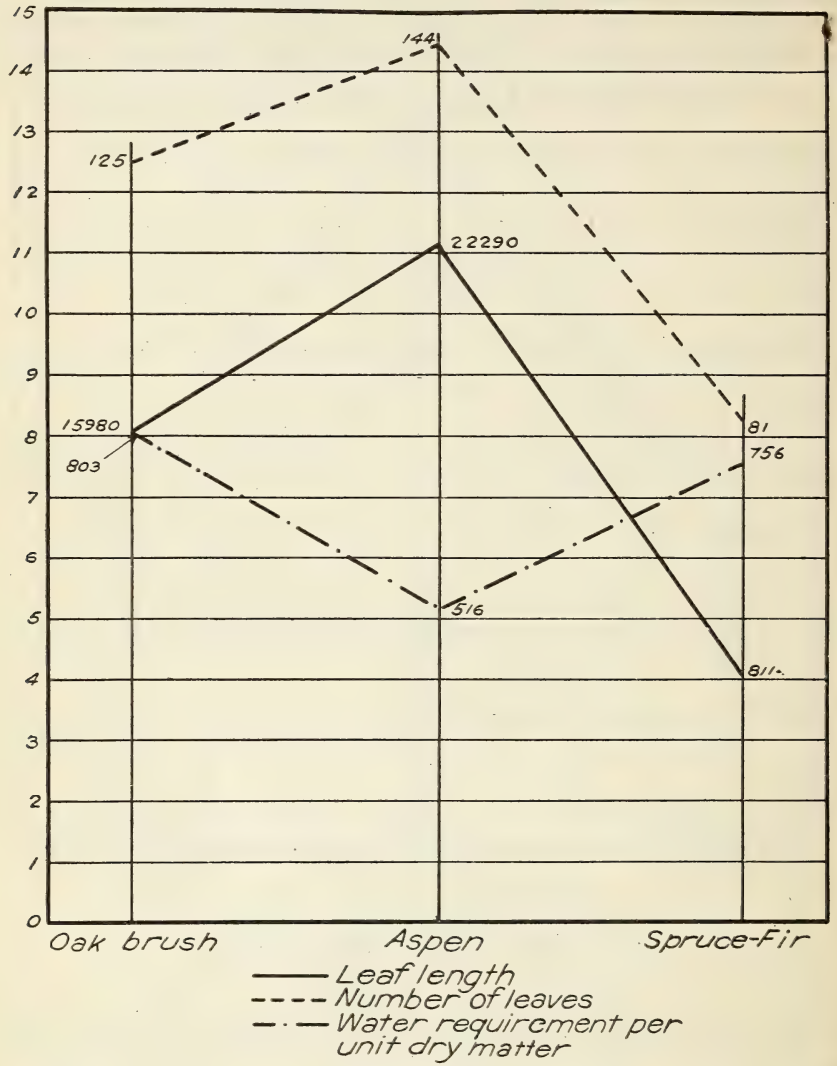


FIG. 23.—Water requirements and vegetative growth of brome grass in the three climatic types.

## THE EFFECT ON PLANT GROWTH OF DIFFERENCES IN THE AMOUNT OF HEAT AVAILABLE IN THE THREE TYPES.

### EFFECT OF TEMPERATURE AS INDICATED BY DIFFERENCES IN WATER REQUIREMENTS BASED UPON STAGE OF DEVELOPMENT AND CONDITION OF CERTAIN AERIAL PARTS.

The total effective heat units and length of growing season in the types studied are such that only in the lowest type do the plants reach

full maturity.[1] In the case of Experimental Series No. 1, in which the standard plants were started simultaneously in all types as soon as the temperature favored growth in the highest type, wheat heads filled well in the aspen-fir type but killing frosts occurred before the caryopsis hardened thoroughly; in the type above, growth was arrested when the heads were still in a developmental stage. Records of these plant specimens, supplemented by those of the late planted batteries (Experimental Series No. 2) afforded data as to the relative water requirements of plants in different stages of development. Because of the difference in age of the plants in the early planted and later planted batteries, the two sets of specimens were really subjected to different environmental conditions, for it is well known that the same weather factors do not affect plants in different stages of development in the same way. For this reason the water requirements of the two sets of plants may not be entirely comparable.

For the purpose of comparisons between the water requirements of the entire tops of wheat and brome-grass specimens, heads included, and tops without the heads, the dry matter of the specimens with and without heads was recorded and the water requirements of each determined. The results are summarized in Table 13.

TABLE 13.—*Relation of water requirements of wheat and brome grass to effective temperatures in climatic types.*

| Types. | Water requirement per unit dry weight. | | Per cent of difference between water requirements without heads and with heads. | Temperature summation above 40° F. |
|---|---|---|---|---|
| | Without heads. | Including heads. | | |
| WHEAT (EXPERIMENTAL SERIES No. 1). | | | | |
| | *Grams.* | *Grams.* | | *Degrees.* |
| Oak-brush | 857 | 626 | 37 | 1,789 |
| Aspen-fir | 358 | 288 | 24 | 1,404 |
| Spruce-fir | 355 | 300 | 18 | 991 |
| WHEAT (EXPERIMENTAL SERIES NO. 2). | | | | |
| Oak-brush | 600 | 504 | 19 | 1,528 |
| Aspen-fir | 407 | 354 | 15 | 1,132 |
| Spruce-fir | 391 | 391 | 00 | 685 |
| BROME GRASS (EXPERIMENTAL SERIES No. 1). | | | | |
| Oak-brush | 1,303 | 803 | 62 | 1,789 |
| Aspen-fir | 736 | 516 | 43 | 1,404 |
| Spruce-fir | 853 | 756 | 14 | 991 |

The above values, platted in figures 24, 25, and 26, exhibit a gradual falling off from the lowest to the highest station in the ratio

[1] Owing to the early maturing qualities of mountain brome grass, this species more nearly reached maturity in all types than did the cultivated plants.

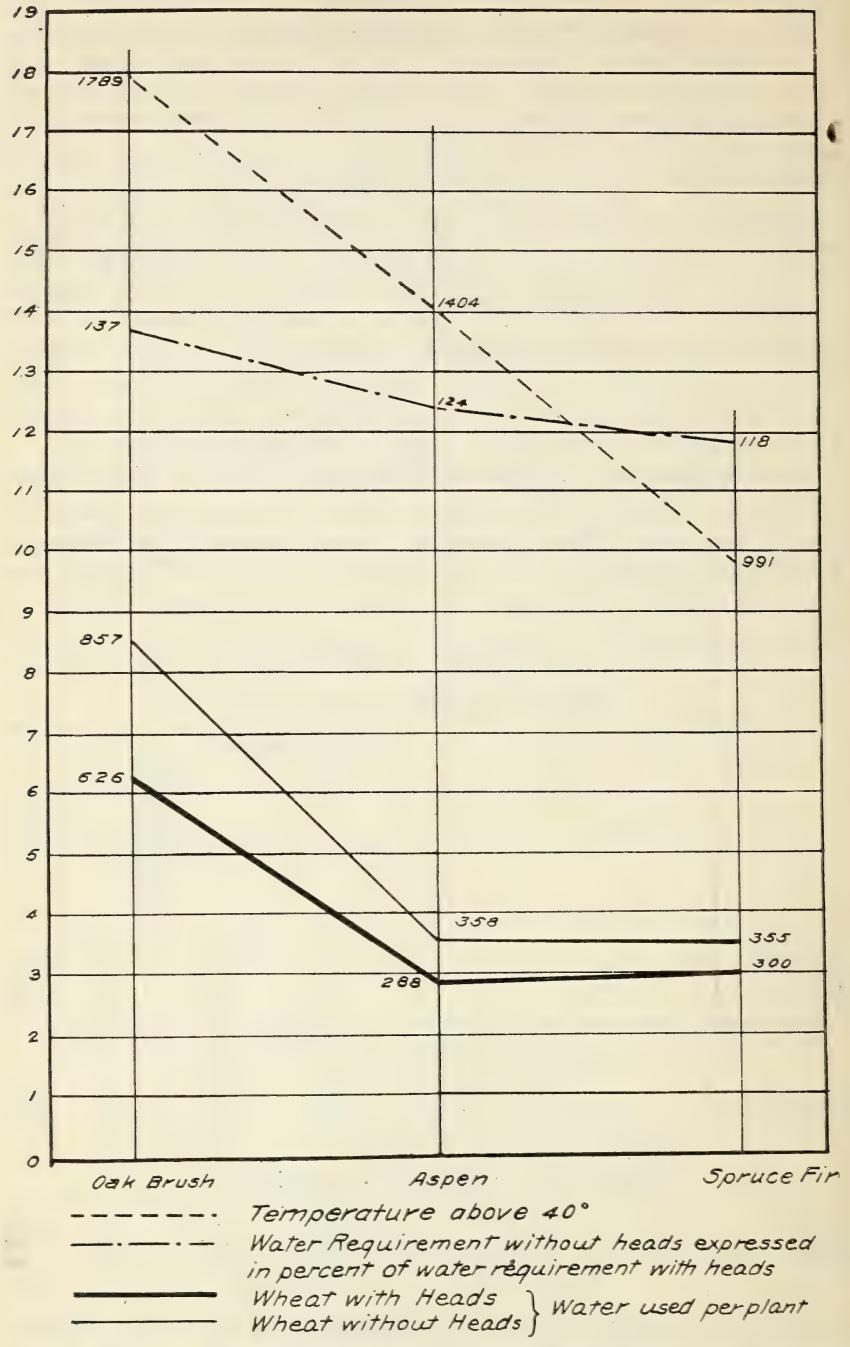


FIG. 24.—Water requirement of wheat based on weight of plant including heads, compared with water requirement based on weight without heads. (Experimental Series No. 1.)

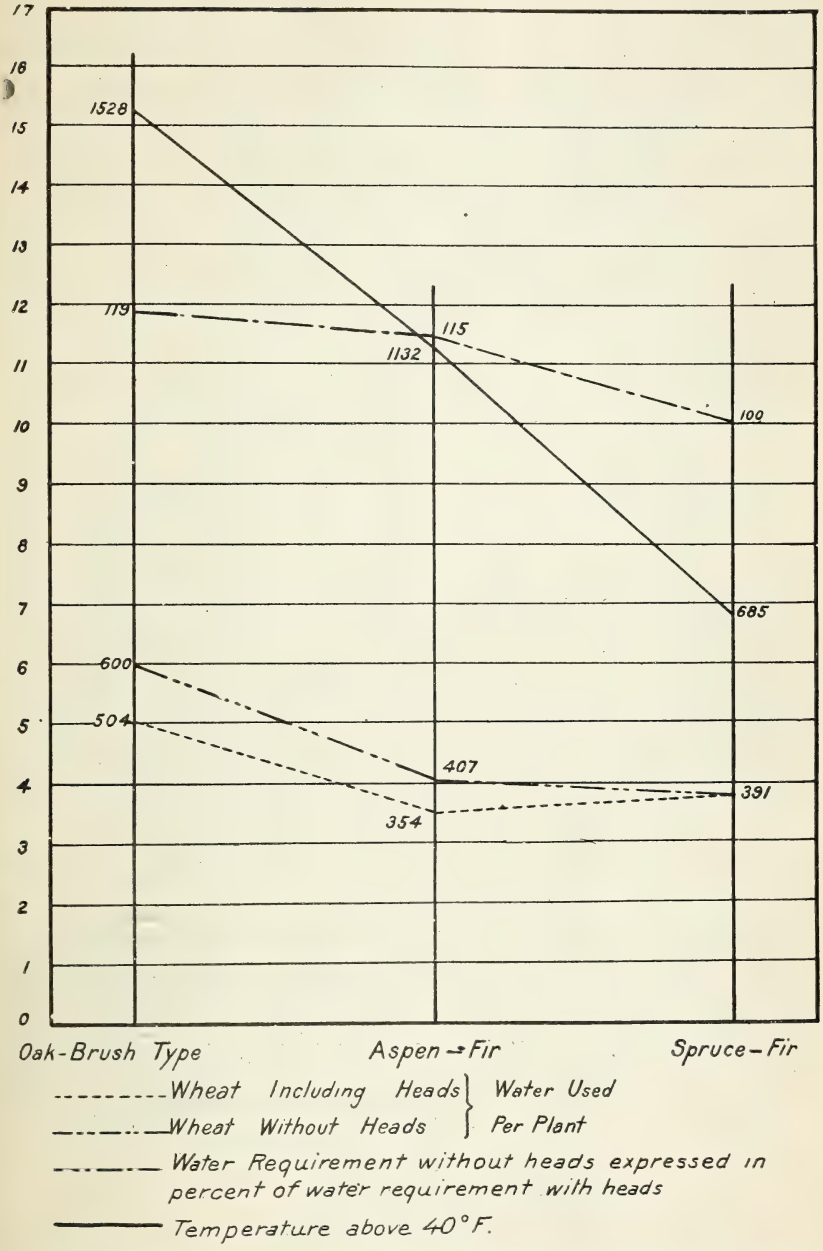


FIG. 25.—Water requirement of wheat based on weight of plant including heads, compared with water requirement based on weight without heads. (Experimental Series No. 2.)

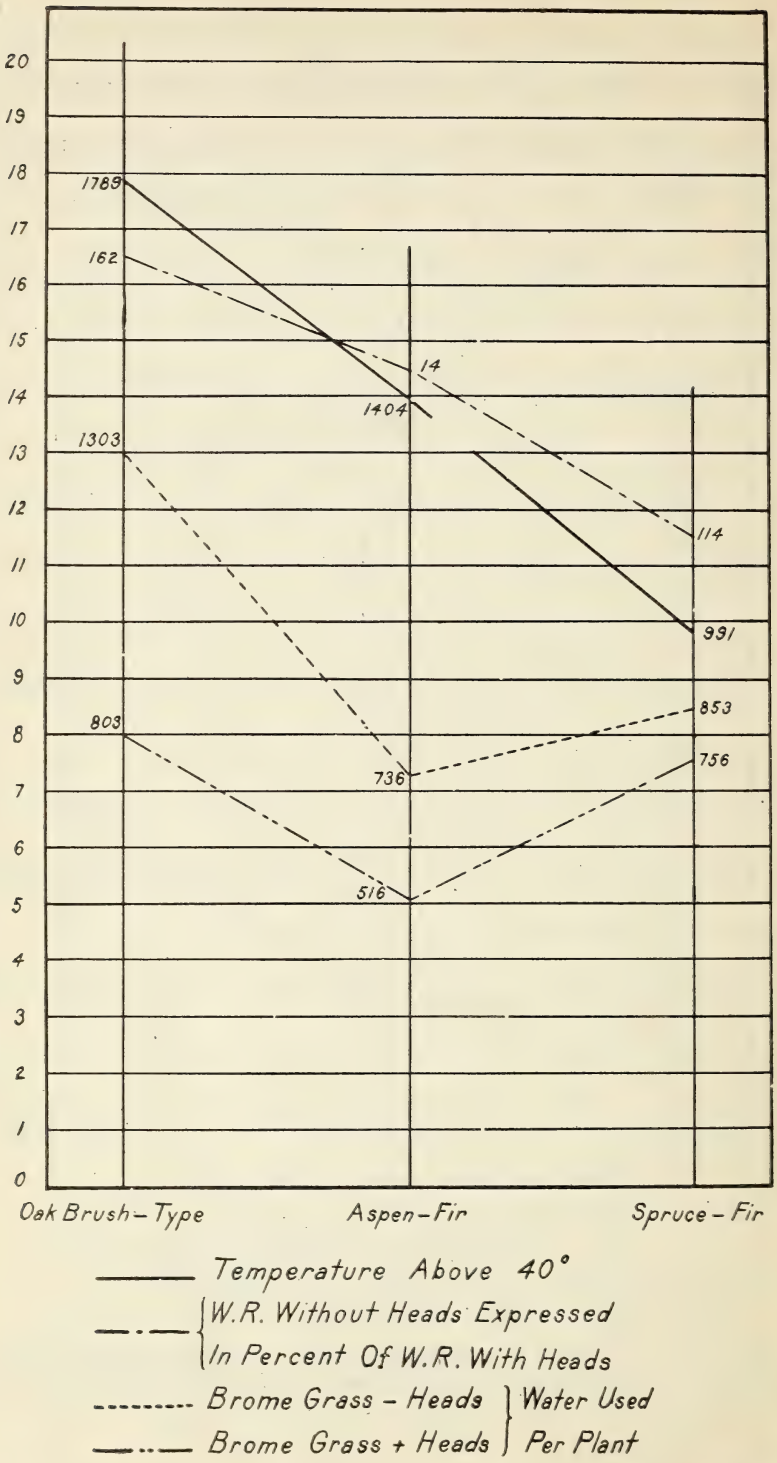


FIG. 26.—Water requirement of brome grass based on dry matter of plant including heads as compared with water requirement based on dry matter without heads.

of the water requirements of wheat and brome grass without heads to those with heads. The difference is rather pronounced. In the case of wheat in the oak-brush type (fig. 24) it is 37 per cent, in the aspen-fir association 24 per cent, and in the spruce-fir type 18 per cent. In the case of less mature wheat specimens (fig. 25) the differences between water requirement of the plants without heads and those plants with heads is 19 per cent, 15 per cent, and zero; for brome grass (fig. 26) it is 62 per cent, 43 per cent, and 14 per cent.

The differences in the water requirement figures serve to show one of the responses of the plants to the different amounts of heat available in the three associations. In the oak-brush type, where the number of heat units is greatest, the plants are matured or nearly so, and a large proportion of the total dry matter of the plants is deposited in the seed heads. At the middle and upper stations, where the summed seasonal temperature efficiency is lower, the plants are less mature, and a correspondingly lower proportion of the total dry matter of the plants is deposited in the heads. This difference in the stage of maturity would seem, then, to account for the difference in the water requirements of the plant with heads and without heads, and the difference itself affords an approximate measure of the relative development and maturity of the plants in the different types.

It is noteworthy that in the figures representing the ratio of the water requirements of the plants based on (1) the tops, including heads and (2) the tops without heads (figs. 24, 25, and 26) the curves in each case fall, from the lowest to the highest type, in a manner roughly proportional to the fall in the temperature summations. This agreement in slope shows that the plants mature more slowly as the number of effective temperature units decreases.

### EFFECT OF TEMPERATURE AS INDICATED BY PERIOD REQUIRED FOR PRODUCTION OF FLOWERS.

Additional data showing the relation of the development of the plant to temperature were obtained by noting the number of days required for the first appearance of flowers in the species grown in the type stations. In each instance temperature summations and average mean temperatures were recorded for each period, the results of which are summarized in Table 14.

TABLE 14.—*Periods required for the production of flowers in the vegetative types and temperature summations and average mean temperatures for the respective periods.*

| Type station. | Peas. | | | Wheat. | | | Brome grass. | | |
|---|---|---|---|---|---|---|---|---|---|
| | Days for appearance of blossom. | Temperature. | | Days for appearance of heads. | Temperature. | | Days for appearance of heads. | Temperature. | |
| | | Above 40° F. | Average daily mean. | | Above 40° F. | Average daily mean. | | Above 40° F. | Average daily mean. |
| | | ° *F.* | ° *F.* | | ° *F.* | ° *F.* | | ° *F.* | ° *F.* |
| Oak-brush | 43 | 1,607 | 64 | 40 | 915 | 69.2 | 39 | 785 | 60 |
| Aspen-fir | 64 | 988 | 56 | 52 | 785 | 55.2 | 52 | 685 | 58 |
| Spruce-fir | 88 | 980 | 51 | 71 | 847 | 52.0 | 63 | 660 | 52 |

Figures 27, 28, and 29 platted from Table 14 show a rather pronounced parallelism in the different figures in the trend of the curves from the lowest to the highest station representing the number of days required for the flowering of the species, on the one hand, and in the curves representing the number of heat units up to time of the production of flowers, on the other. Provided no other factor was operative in holding back growth in the case of the plants in question it would appear that temperature was the controlling factor in this instance. In the case of peas, flowers appeared 21 days earlier in the oak-brush type than in the aspen-fir type and 45 days earlier than in the spruce-fir type, the period between planting and flowering in the spruce-fir type being more than twice as long as the corresponding period in the oak-brush type. Wheat spikes appeared in the lowest type in 40 days; while in the central and highest types they began to show 12 and 31 days later, respectively. In the case of mountain brome grass, panicles showed in 39 days in the lowest type; but in the central station they did not begin to show until 13 days later and in the spruce-fir type 24 days later. One of the most interesting facts brought out in these observations is that in spite of the fewer days required for flowering in the oak-brush type a great many more flowers were produced than in the other types. In the case of wheat, for example, 40 per cent more heads appeared in the oak-brush than in the aspen-fir type, and over 100 per cent more than in the highest type.

The fact that there is very little slope in the effective temperature summation curves and in the average daily mean temperature curves in figures 27, 28, and 29 shows that practically the same number of heat units were required in each type for the production of flowers. On the physiological basis of temperature summation for the entire season, as has previously been pointed out, there were notably more heat units in the lowest type. The lowest temperature efficiency was

recorded in the spruce-fir type, while in the central type the physiological temperature efficiency was intermediate. Since a habitat with low-growing temperatures requires a greater number of days for the

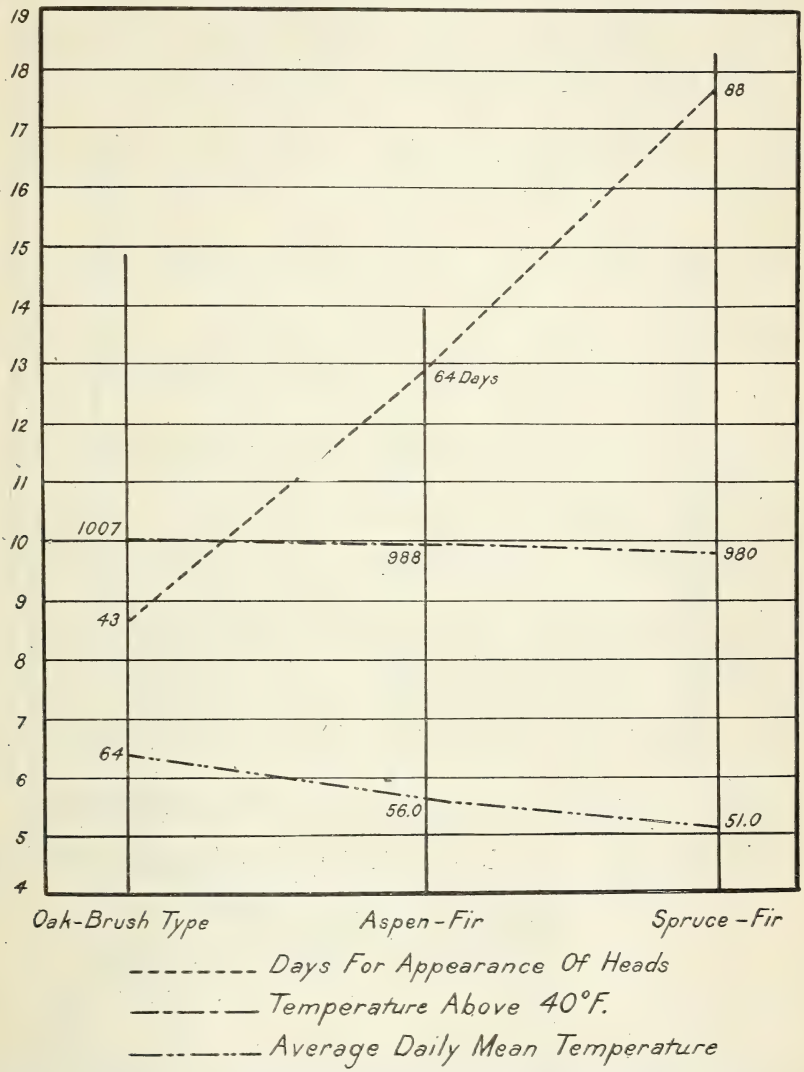


FIG. 27.—Relation of temperature to time of first appearance of blossoms in peas.

plant to reach a given stage of maturity than a warmer situation, it is evident that the physiological temperature indices would be in inverse ratio to the time required to bring the plant to a given stage of maturity.

The difference in the time for the plants to reach approximately the same stage of maturity in the type stations may account, in part at least, for the difference in the character and composition of the vegetation in the respective types as well as for failures to establish exotic and indigenous species adapted to types of higher effective temperatures. In the spruce-fir type only those species which can com-

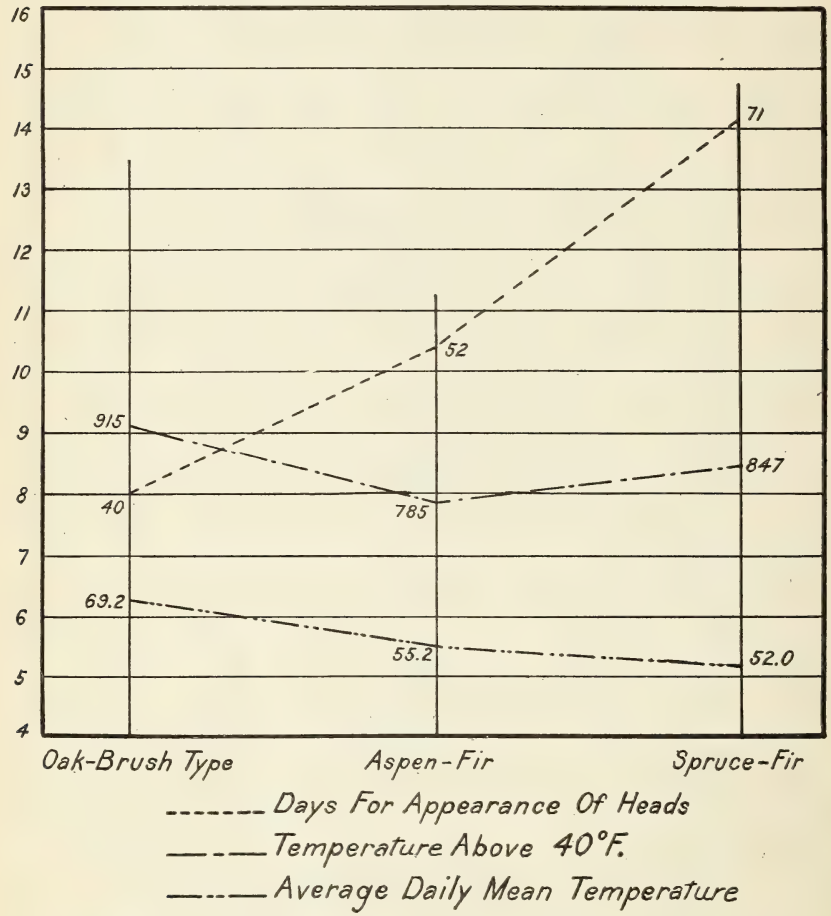


FIG. 28.—Relation of temperature to time of first appearance of heads of wheat.

plete their development to maturity in minimum time, provided, of course, that their perpetuation is dependent wholly or primarily on seed, are conspicuously in evidence and of economic importance. This tendency toward early maturity is evident, for example, in the case of mountain brome grass, less days being required in all type stations for its flower production than for that of peas and wheat.

EFFECT OF TEMPERATURE AS INDICATED BY WATER REQUIREMENT PER UNIT OF LEAF AREA.

The water requirements per unit of area of the chief food manufacturing agents of plants—the leaves—may be used as an index of the

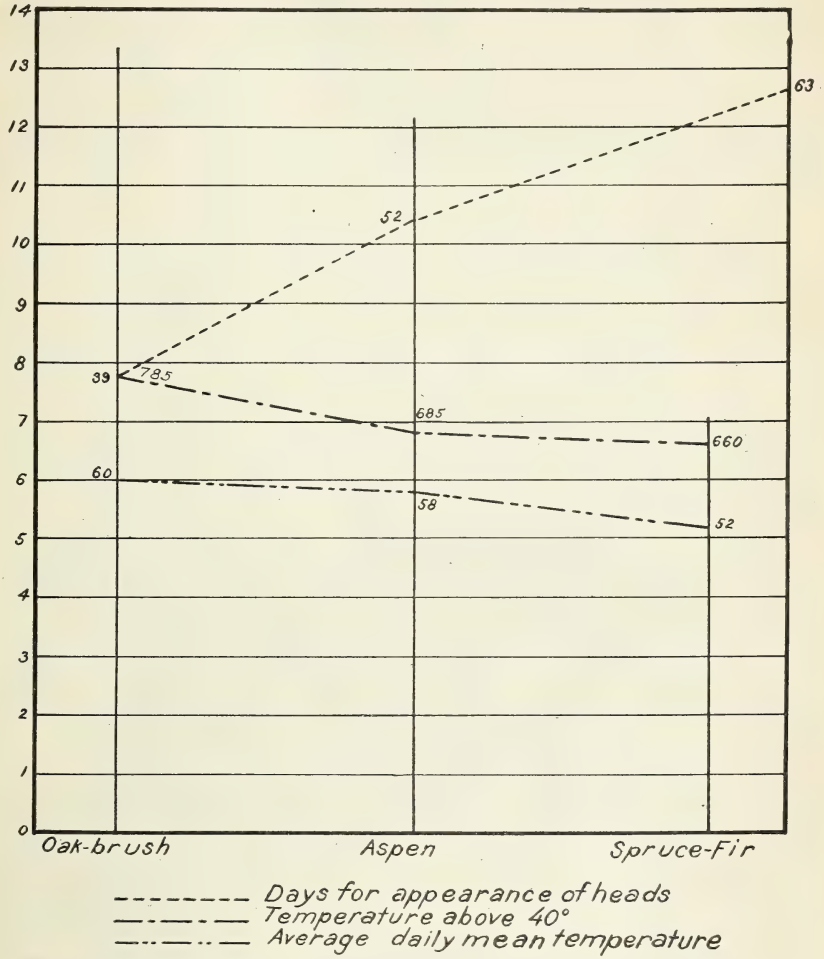


FIG. 29.—Relation of temperature to time of first appearance of heads of brome grass.

efficiency of the leaves as users of water. The leaf length is used instead of actual leaf area in the data given below, since, as has been previously shown, it is proportional to the actual area.

TABLE 15.—*Water requirements per millimeter of leaf length of wheat and brome grass in type stations.*

| Type. | Temperature above 40° F. | Per cent difference in water requirements between wheat and brome grass. | Water requirements per millimeter leaf length. | | Physiological temperature efficiency. |
|---|---|---|---|---|---|
| | | | Wheat. | Brome grass. | |
| | *Degrees.* | | *Grams.* | *Grams.* | *Index.* |
| Oak-brush | 2,002 | 312 | 1.000 | 0.321 | 2,706.2 |
| Aspen-fir | 1,404 | 195 | .526 | .273 | 1,560.5 |
| Spruce-fir | 991 | 127 | .407 | .319 | 730.5 |

Wheat uses nearly twice as much water per millimeter leaf length in the oak-brush type as in the aspen-fir type, and more than twice as much as in the spruce-fir type (fig. 30). In other words, water appears to be used most conservatively by a unit of wheat-leaf area in the type showing the lowest physiological temperature efficiency and temperature summation above 40° F., and most extravagantly in the type of highest temperature efficiency. Hence the curve representing the water requirement of wheat and the temperature summation curves fall from the type lowest in elevation to that of highest altitude in the same general way.

In the case of brome grass the water requirement of the leaves is found to be practically the same in all types in spite of the difference in the climatic conditions and in the stage of development of the plants. The reason for this dissimilarity between the two species is not entirely clear, but it may be related to the fact that mountain brome grass does not naturally inhabit the oak-brush type, though, indeed, the specimens observed appeared to develop normally.

In all instances a given leaf area of brome grass has a lower water requirement than wheat. Notwithstanding this fact, however, the water requirement per unit of dry matter for the plant as a whole, as previously shown, is greater for brome grass than for wheat. This is largely accounted for by the fact that the aerial part of mountain brome grass consists essentially of leaf blades, while a large proportion of the aerial dry matter of wheat is made up of stems and heads, the transpiration from which is low as compared with leaf surface. This relation between the water requirements of leaves of the two species is further shown by the curve representing the water requirement per millimeter of leaf length of wheat expressed as a percentage of the water requirement per millimeter of leaf length of brome grass. These percentages, which are 312 in the oak-brush type, 195 in the central station, and 127 in the spruce-fir type, indicate that wheat becomes relatively more efficient in the use of water as compared with brome grass as the temperature falls.

Furthermore, the curve representing these percentages bears an intimate agreement with both of the temperature summation curves. This increased conservatism in the use of water in wheat leaves may,

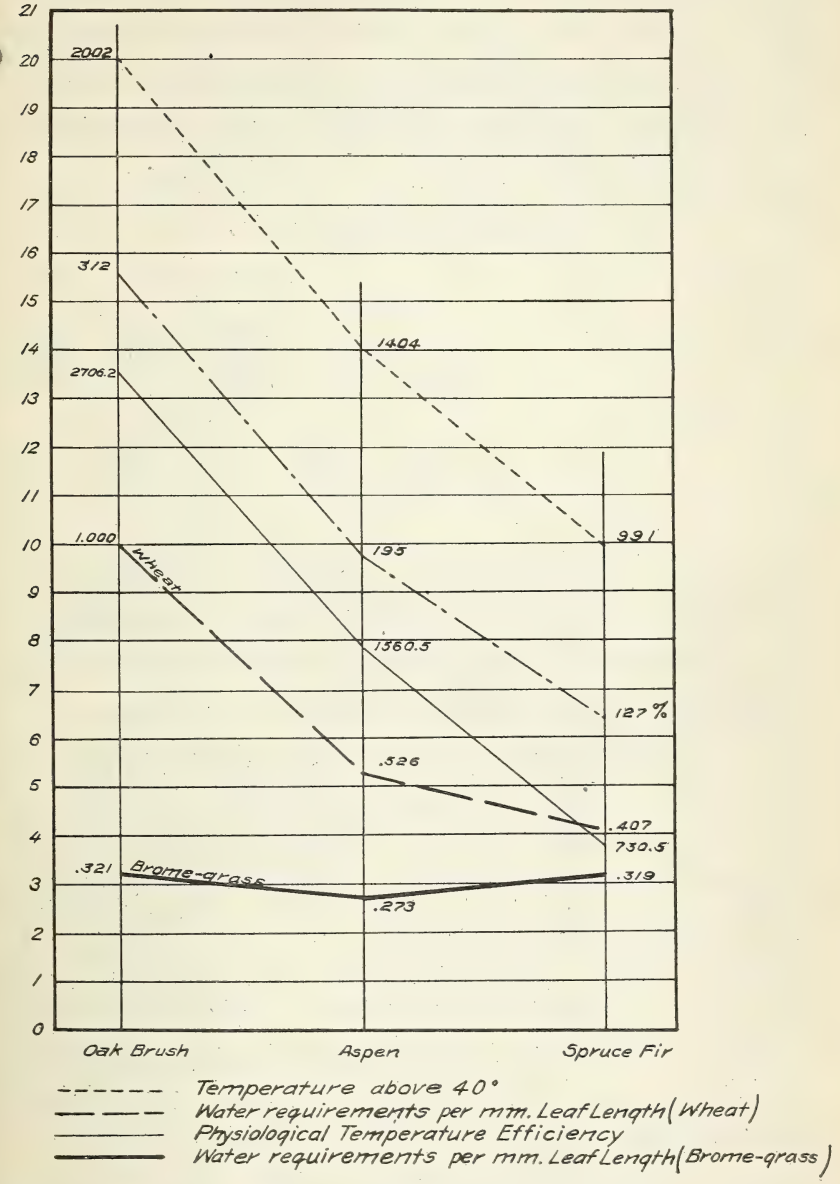


FIG. 30.—Water requirements per unit (1 mm.) of leaf length of brome grass and wheat.

in a way, account for the high yielding qualities of wheat, other conditions remaining the same, in regions where the summers are relatively cool.

## EFFECT OF EVAPORATION AND TEMPERATURE ON THE PRODUCTION OF DRY MATTER PER UNIT OF LEAF AREA.

Quite as significant as the difference in water requirements per unit of leaf area in the respective types is the effect of climatic conditions on the efficiency of the leaves as manufacturing agents. This has been calculated for wheat and brome grass, the same specimens being employed as were used in deriving the water requirement data. The summations are given in Table 16 and in figure 31.

TABLE 16.—*Dry matter produced per millimeter of leaf length of wheat and brome grass in the type stations.*

| Type. | Dry weight. | | Per cent difference in dry weight of wheat and brome grass. | Evaporation summation. | Physiological temperture efficiency. |
|---|---|---|---|---|---|
| | Wheat. | Brome grass. | | | |
| | *Grams.* | *Grams.* | | *cc.* | |
| Oak-brush | 0.00161 | 0.00040 | 403 | 4,550.0 | 2,706.2 |
| Aspen-fir | .00182 | .00054 | 338 | 2,780.3 | 1,560.5 |
| Spruce-fir | .00136 | .00042 | 324 | 4,251.3 | 730.5 |

Both curves in figure 31 representing the dry matter per unit of leaf area show a maximum for the central type, the greatest concavity upward occurring in the curve for wheat. This species also shows a slightly greater production in the oak-brush type than in the spruce-fir type. In brome grass the reverse occurs, but in neither instance is the difference particularly marked.

It is significant that the curve representing the production of dry matter is opposite in slope to the curve showing the evaporating power of the air. The data indicate that evaporation decreases the rate at which the leaves manufacture food material, and the similarity in the production of dry matter in the case of both species in the three types may thus be accounted for by corresponding similarities in the evaporation conditions.

Another interesting parallelism is derived by dividing the dry matter per unit of leaf length produced by wheat by the quantity produced by brome grass. In this instance the curve is seen to fall from the lowest to the highest type in the same general direction as the physiological temperature efficiency curve. This apparent correlation between temperature and the efficiency of the leaves as manufacturing agents is of value, of course, only if it may be assumed that the physiological index affords a reliable expression of the relation between the temperature and the plants here dealt with.

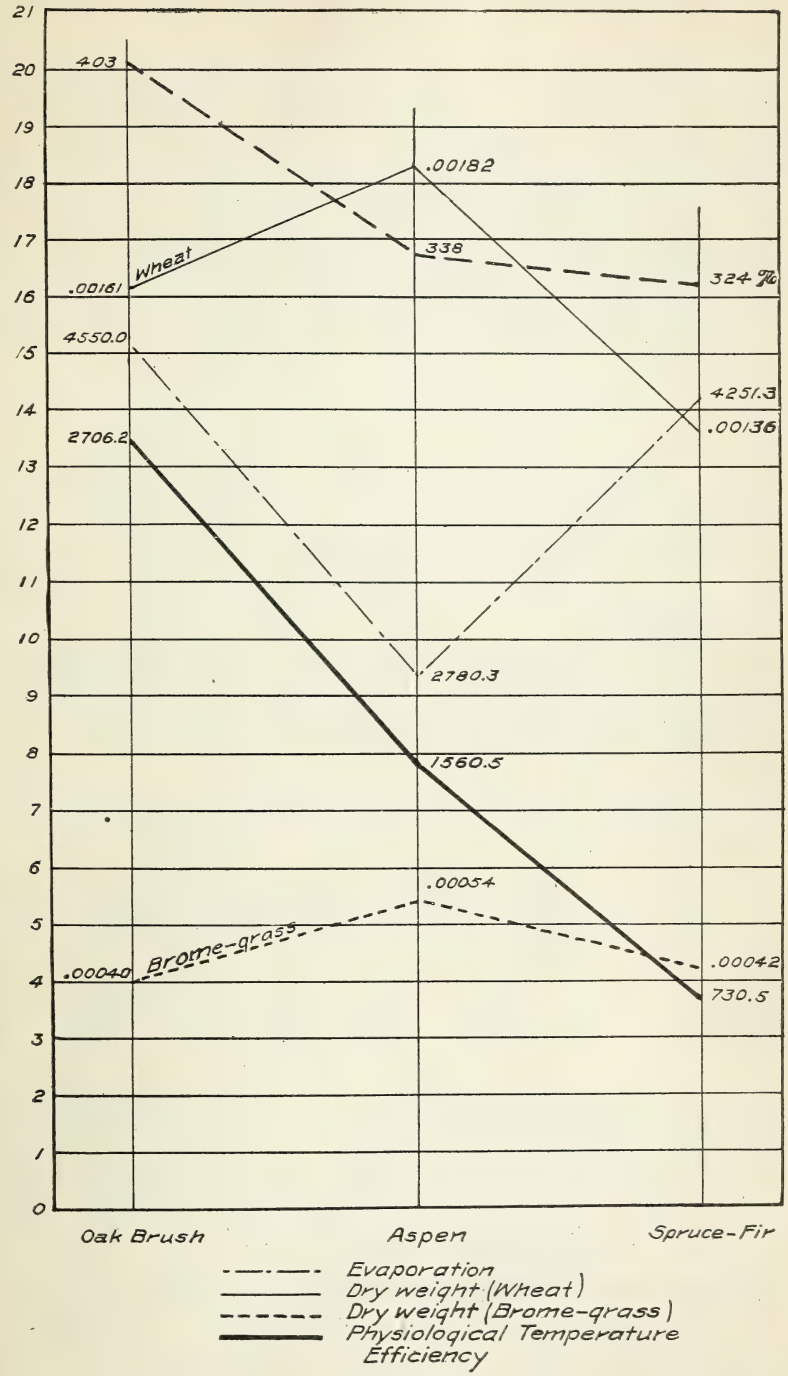


FIG. 31.—Dry matter produced by one millimeter of leaf length by brome grass and wheat (heads included).

## EFFECT OF EVAPORATION AND TEMPERATURE ON THE GROWTH OF THE PLANT AS A WHOLE.

It has been shown that the efficiency of the leaves, both as users of water and as producers of material, is much influenced by climatic conditions. The true significance of this fact, however, can be fully understood only when the development of the plant as a whole, including stem height, total seasonal and periodic leaf expansion, and similar activities, is correlated with the controlling climatic factors.

Temperature and evaporation are, as the preceding discussion has shown, undoubtedly the limiting factors in the locality in which this investigation was conducted, and hence it is the chief aim to show physiological activities in relation to these factors.

### EFFECT OF EVAPORATION AND TEMPERATURE ON THE GROWTH OF WHEAT.

Since more measurements were taken in the case of wheat than of the other species, wheat is here selected to show correlations between its development and temperature and evaporation. In this connection it should be stated that the correlations obtained between climatic factors and growth of wheat hold generally for the other species employed.

Four sets of measurements of wheat and the daily temperature and evaporation obtained for the period of growth concerned were recorded in each type station simultaneously. The data are summarized in Table 17 and platted in figure 32.

TABLE 17.—*Growth of wheat as related to evaporation and temperature in type stations.*

| Type. | Evaporation. | Temperature above 40° F. | Average stem length. | Dry weight per plant. | Leaf length. | Water used per plant. |
|---|---|---|---|---|---|---|
| | *cc.* | | *Mm.* | *Grams.* | *Mm.* | *Grams.* |
| Oak-brush | 39,563 | 1,789 | 1,100 | 6.33 | 3,938 | 3,949 |
| Aspen-fir | 27,803 | 1,404 | 1,018 | 15.61 | 8,560 | 4,499 |
| Spruce-fir | 42,513 | 991 | 830 | 7.19 | 5,221 | 2,147 |

In figure 32 the direction of slope of the graphs representing total leaf length and average dry weight per plant is similar, a pronounced convexity upward occurring in the aspen-fir association. These measurements, then, are in inverse proportion to the evaporation. On the other hand, no apparent correlation exists between the curves representing the average stem length and evaporation. Since the curve of evaporation bears no distinct correlation to the temperature summation curve, it would appear that the height growth, or elongation of the plant, is determined more by the temperature than by the evaporation, the factor which apparently determines elongation and ex-

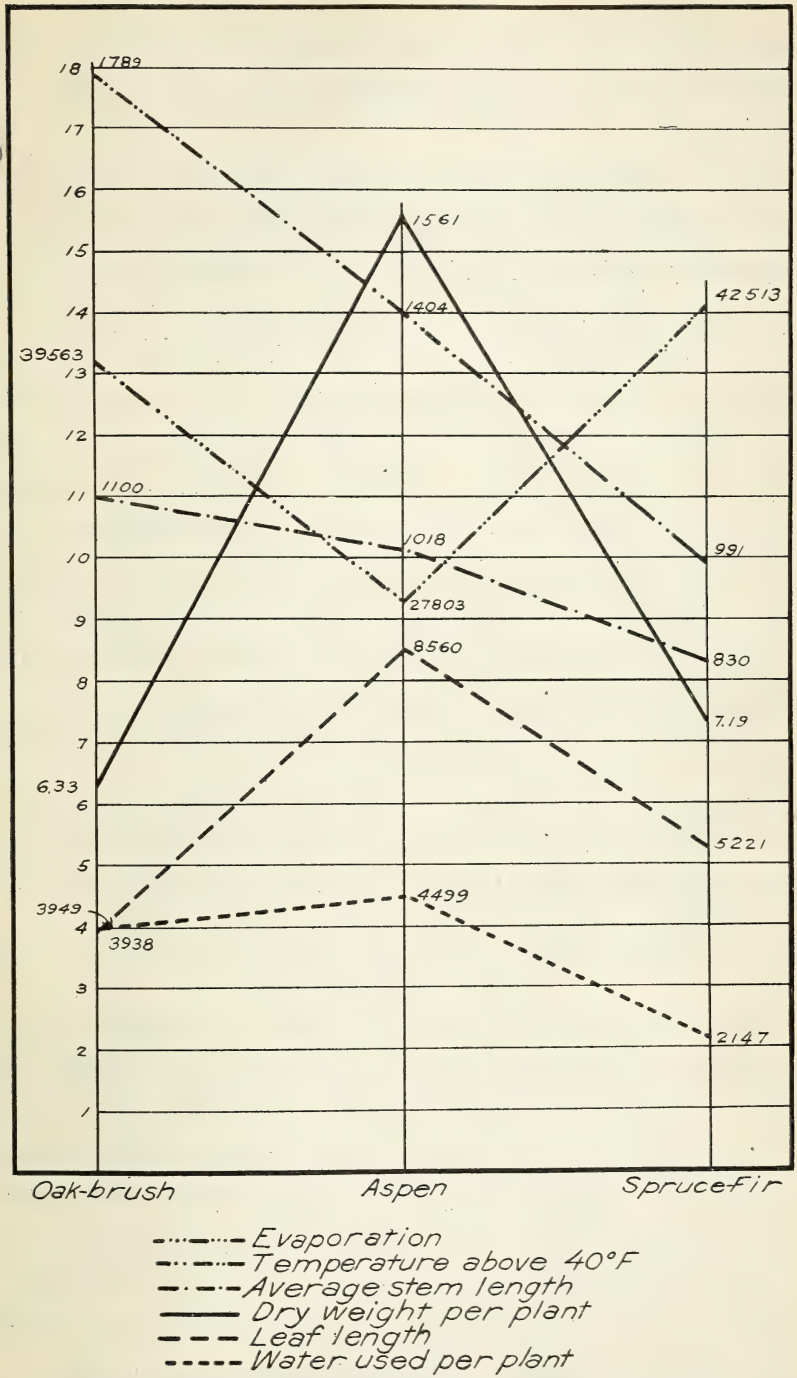


FIG. 32.—Comparison between climatic factors and the growth of wheat.

pansion of the leaf. The curve representing the water used per plant, on the other hand, is more or less intermediate in slope between the temperature and evaporation summation curves, and it is indicated that the water used per plant is determined both by temperature and evaporation.

The above figures are based on average measurements of 20 specimens in each type, but the data may not be adequate to justify the statement that leaf elongation and expansion of plants in general are locally, and under similar conditions, controlled more by evaporation than by temperature. Where the evaporation is especially high owing chiefly to factors other than high-wind movement, however, as in the oak-brush type, the data appear to warrant the conclusion that evaporation is the limiting factor in leaf expansion and consequently in the production of dry matter and other physiological activities of economic importance. This conclusion is further substantiated by the data presented in figures 30 and 31, showing on the one hand relatively high water requirement and on the other a correspondingly low production of dry matter in a unit of leaf area in the oak-brush type. The correlation between high evaporation and low production of dry matter may be explained either by the lack of proper turgor in the leaf cells during the long diurnal periods of high transpiration, or by the fact that egression of water molecules from the stomata and cells adjacent thereto is so great as to prevent free ingression of carbon dioxide essential to photosynthesis.

From the lower border of the aspen-fir type (about 8,000 feet elevation) throughout this association and in the less exposed sites of the spruce-fir type temperature and evaporation may exert equal effect on the plant.

### EFFECT OF EVAPORATION AND TEMPERATURE ON SEASONAL MARCH OF GROWTH RATES OF WHEAT AND BROME GRASS.

While a measure of the relation of climate to the development of vegetation may be integrated by summarizing the climatic data and recording the dry matter produced by comparable plants during the entire growing season, the relation may best be known through concrete comparisons made at more or less regular intervals throughout the season. This is especially true of the more elevated regions, where weather within a season is subject to wide variation. Even if the relations between plant growth and weather were known, however, the factors affecting growth vary in a more or less unpredictable manner, so that the yield of a given crop could not be correctly judged much in advance of actual harvest.

If the assumption that leaf-expansion rate is retarded by evaporation is correct, the graph of evaporation platted period by period

for the season at any given station should show an opposite slope to the corresponding graph of leaf-expansion rate. In order to determine whether such a relation exists, the rate of leaf expansion was calculated for the periods for which plant measurements were made, as was also the evaporation rate.

The values of seasonal march of leaf-growth rate given in Table 18, and graphically shown in figures 33, 34, and 35, represent average daily increase in length per leaf for the various culture periods. This quantity was obtained for each period by dividing the total leaf

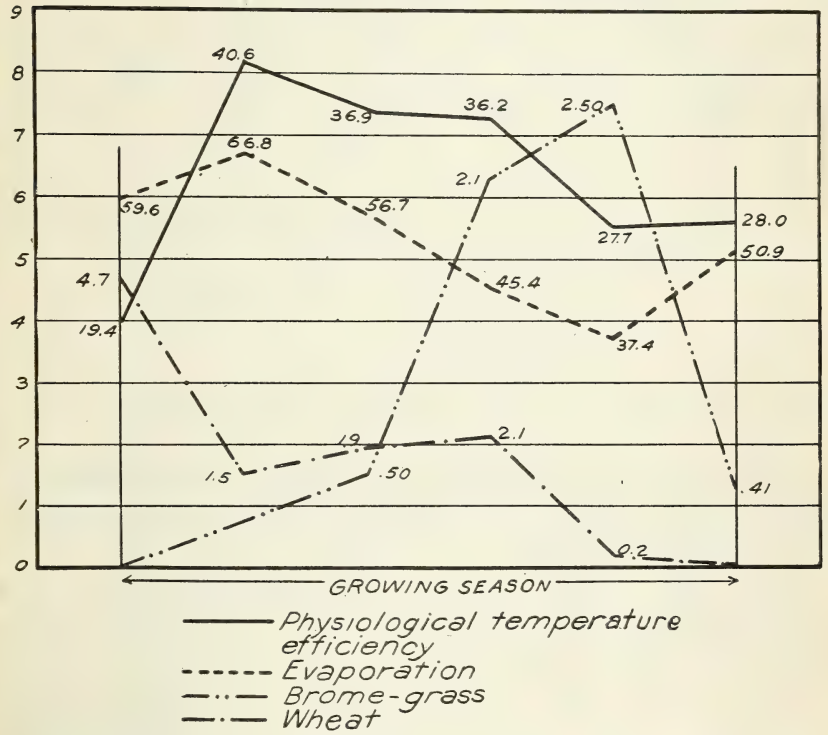


FIG. 33.—Periodic relation between leaf expansion, evaporation, and temperature, oak-brush type.

length produced up to the time of measurement by the total number of leaves, thus giving the average length per leaf. The increase in the average length per leaf of the plants from period to period was then determined by subtracting from each of the average leaf-length values the corresponding value of the preceding period. Since the periods for which measurements were taken varied somewhat in time, these increases, in order to make them comparable, were reduced to daily rates by dividing each increase in average leaf length by the number of days in which the increase took place. The physiological

temperature index and the evaporation rate were also expressed as average daily rates in order to make these climatic factors comparable to the plant measurements. The data were recorded prac-

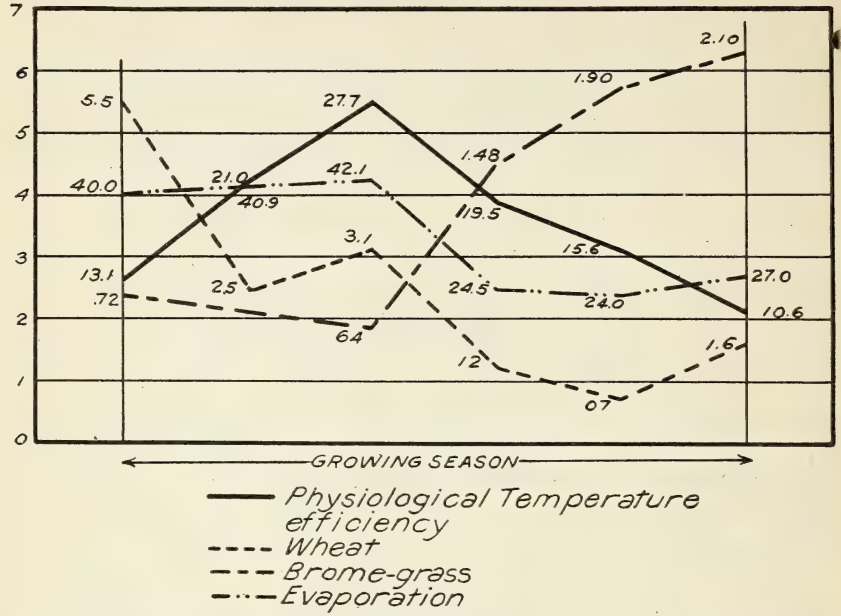


FIG. 34.—Relation between increments of leaf expansion, evaporation rate, and temperature, aspen-fir type.

tically simultaneously at about 10-day intervals in each association. The first measurements here recorded are for June 22—10 days after establishing the potometers.

TABLE 18.—*Effect of evaporation and temperature on leaf expansion of wheat and brome grass in type stations at about 10-day intervals, beginning June 22, through growing season.*

| Association. | Brome grass. | Wheat. | Physiological temperature efficiency. | Evaporation summation. |
|---|---|---|---|---|
| | *Mm.* | *Mm.* | | *cc.* |
| Oak-brush | 0 | 4.7 | 19.4 | 59.6 |
| | | 1.5 | 40.6 | 66.8 |
| | .50 | 1.9 | 36.9 | 56.7 |
| | 2.10 | 2.1 | 36.2 | 45.4 |
| | 2.50 | .2 | 27.7 | 37.4 |
| | .41 | .0 | 28.0 | 50.9 |
| Aspen-fir | .72 | 5.5 | 13.1 | 40.0 |
| | | 2.5 | 21.0 | 21.0 |
| | .64 | 3.1 | 27.7 | 42.1 |
| | 1.48 | 1.2 | 19.5 | 24.5 |
| | 1.90 | .7 | 15.6 | 24.0 |
| | 2.10 | 1.6 | 10.6 | 27.0 |
| Spruce-fir | 2.00 | 1.90 | 5.8 | 50.0 |
| | 1.10 | .30 | 9.8 | 83.1 |
| | 1.90 | 2.40 | 12.5 | 59.6 |
| | 2.30 | 2.80 | 10.8 | 38.8 |
| | 6.50 | 2.10 | 7.4 | 30.0 |
| | 6.10 | .85 | 5.7 | 49.0 |

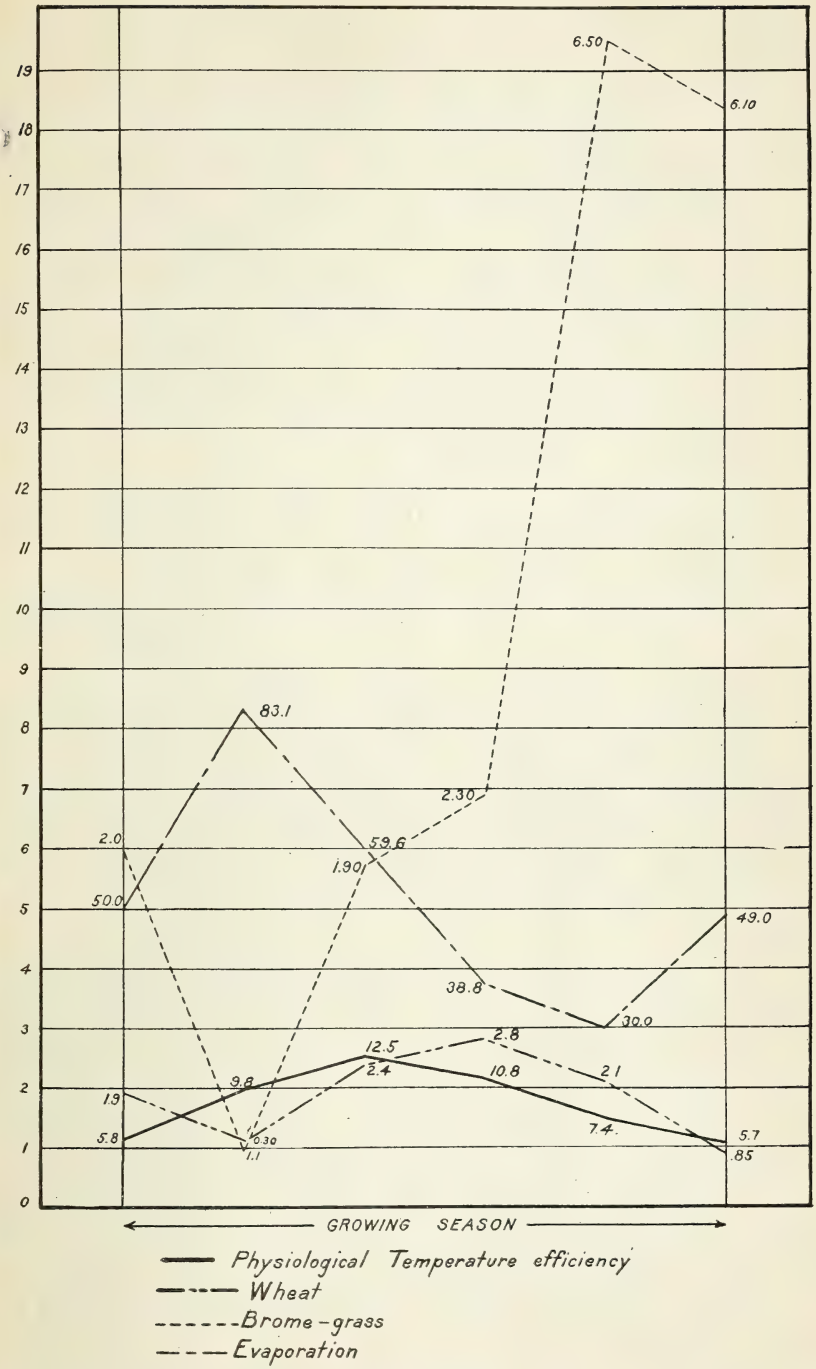


FIG. 35.—Relation between increments of leaf expansion rate and temperature, spruce-fir type.

The curves (figs. 33, 34, and 35) representing leaf expansion, in some instances at least, follow the temperature curves, but in general slope in opposite direction to the curves portraying the evaporation rate. Exception to the latter occurs in the case of wheat in the aspen-fir type; but data already presented have shown that evaporation is not a limiting factor for this plant in this type. Also it will be seen that growth toward the end of the season does not in all cases bear an inverse relation to evaporation. As an explanation of this fact it should be stated that the leaf growth is rapidly declining at that time, because of the approach of maturity of the plants. On the other hand, there appears to be no consistent correlation between growth increments and temperatures. The agreements that do occur also show a direct correlation between growth and evaporation, and hence it may be concluded that the temperature and growth relations recorded are more or less incidental.

Considering the graphs more in detail, in the case of figure 33 the leaf increment curves of both species in practically all instances have concavities opposite in direction to those of the curve representing the evaporation. It should be stated that no growth data were obtained for brome grass in the second period of measurements, and therefore the slope of the line at that point is not in agreement with the growth curve for wheat, nor is it in opposition to the slope of the evaporation curve. In the case of wheat, the leaf expansion curve and the evaporation values platted for the first three periods show inverse relation. Between the fourth and fifth periods there is a slight disagreement in these values, but between the fifth and sixth periods the leaf measurement and evaporation curves again show opposite trend. The leaf increment curve for brome grass, on the other hand, is in inverse proportion to the evaporation in all instances.

As would be expected, where evaporation is unusually high, as in the oak-brush type, temperature in general is high, and these factors usually run more or less parallel. This being the case, it is hardly to be expected that the growth increments would follow the physiological temperature indices. As is well known, the growth rate increases with increase in temperature up to the optimum requirement of a given species. In the oak-brush type there is reason to believe that the temperature not uncommonly exceeds the optimum requirements of the species observed. The lack of correlation between growth rate and temperature in the oak-brush type, then, would seem to strengthen the evidence that the evaporation in that association is the determining factor in the rate of elongation as well as ultimate expansion of the leaf.

In figure 34, in which similar data are given for the aspen-fir type, wheat, except in one instance follows the evaporation curve,

hence to some extent that of the temperature; while in the case of brome grass the leaf expansion curve slopes opposite to the evaporation curve. In the central type, the evaporation being less than in the lowest and the highest types (fig. 8), in no instance has proved a limiting factor for the type in question so far as concerns the physiological activities of wheat. In the case of brome grass, however, the contrary is true. The reason for the difference in the response of these species is not obvious.

In the spruce-fir type figure 35 shows that the leaf increment values in the case of brome grass are in inverse proportion in every instance to those of evaporation.[1] Hence, between the first and third periods, when the highest rate of evaporation occurs, is recorded the lowest rate of leaf expansion for the entire period; and between the fourth and sixth periods, which marks the lowest rate of evaporation, by far the highest growth rate is recorded. The rates of leaf expansion in wheat likewise show inverse relation to evaporation, though less pronounced than the leaf-expansion rates of brome grass, with the exception of the next to the last period. This disagreement, however, is explained by the fact that the wheat specimens were approaching maturity and the growth rate was, therefore, beginning to decline.

As in previous instances, the curve showing the growth rate of wheat in the spruce-fir type seems to follow, in a general way, the daily temperature curve, but this is evidently more or less incidental. In order to determine these relations more definitely, averages of daily leaf increment of wheat and of temperature and evaporation were computed for the season as a whole, the results of which are platted in figure 36. From these curves it is evident that leaf increment of wheat is in inverse proportion to evaporation, no obvious relation to temperature being shown. This relation is also found to hold in the case of brome grass.

To sum up the facts regarding the relation of leaf expansion to evaporation and temperature: The daily rate of growth of the species studied, as well as the total leaf surface produced, varies inversely as the evaporation, except in the case of the daily rate for wheat at the middle station. Evaporation in the aspen-fir type is lower than in the types immediately above and below. As a limiting factor the evaporation may be declared transitional in a sense— that is, it may determine growth rate periodically or seasonally in one species, but not distinctly so in another. Since temperature and evaporation are admittedly more or less interrelated, it is difficult to separate

[1] As previously shown, the high evaporation in the spruce-fir type is chiefly accounted for by high wind movement.

them; consequently, their individual effect on the activities of the plant can not be definitely declared in all instances.

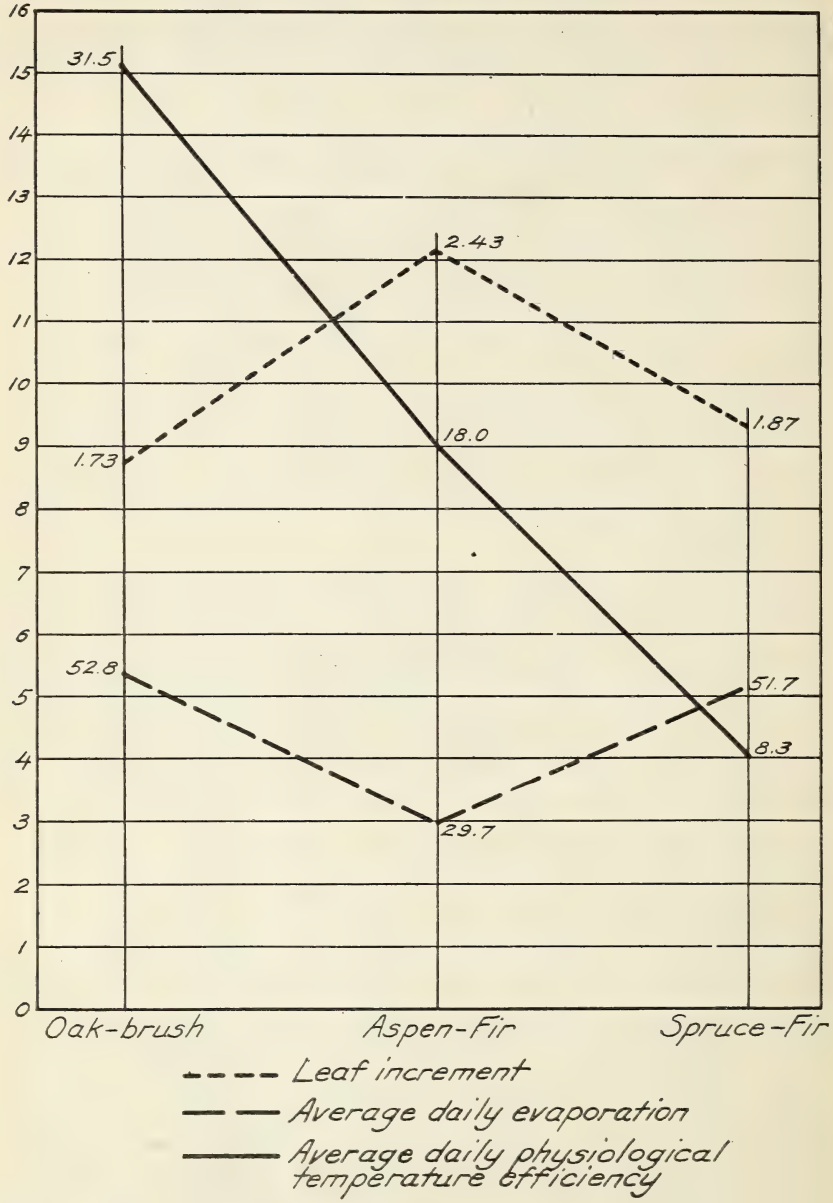


FIG. 36.—Average daily increment in leaf expansion of wheat throughout season compared with evaporation and temperature in type stations.

EFFECT OF TEMPERATURE AND EVAPORATION ON WATER REQUIREMENTS OF PLANTS.

Since the rate of growth and production of dry matter by plants appear to be controlled chiefly by evaporation and temperature, so

far as physical factors in the locality here dealt with are concerned, it appeared pertinent to determine whether or not the water requirement is also correlated with the factors mentioned. The value of data showing the relative water requirement of different plant species has been demonstrated by numerous investigators. The climatic factors that chiefly affect the rate of dissipation of water through transpiration, on the other hand, have until very recently received relatively little attention, although such researches would appear to be of profound economic importance. If it were known, for instance, that in a region of limited rainfall the evaporation was largely responsible for the high transpirational demand and consequently the high water requirement of a given plant, habitats might be selected where vegetation, natural barriers, or other features would afford protection against excessive evaporation. Likewise, if temperature were the factor determining the water requirement, cool north and east slopes, or possibly partially shaded sites might be selected at least at lower elevations and failure of crop production thus avoided.

In order to determine the relation of water requirement of these plants to evaporation and temperature in the type stations, the water used per unit of dry matter by wheat, peas, and brome grass, through practically the entire growing season, was divided by the evaporation for the corresponding period. Tabular and graphic presentation of the results follows.

TABLE 19.—*Effect of temperature and evaporation on water requirements of plants grown in type stations.*

| Type. | Species. | Physiological temperature efficiency. | Water requirement per unit dry matter. | Evaporation for period of growth. | W. R. / E. |
|---|---|---|---|---|---|
| | | | *Grams.* | *c c.* | |
| Oak-brush | Wheat | 2,473.7 | 626 | 3,956.3 | 0.158 |
| | Peas | | 779 | | .197 |
| | Brome grass | | 803 | | .203 |
| Aspen-fir | Wheat | 1,560.3 | 288 | 2,780.3 | .104 |
| | Peas | | 368 | | .132 |
| | Brome grass | | 516 | | .186 |
| Spruce-fir | Wheat | 730.5 | 300 | 4,251.3 | .071 |
| | Peas | | 345 | | .081 |
| | Brome grass | | 756 | | .178 |

As has been shown in previous graphs, the physiological temperature efficiency is highest in the oak-brush type, the curve dropping in practically a straight line to the central and highest types. The quotients of the values derived by dividing the water requirement per unit weight of dry matter for the respective types by the evaporation for each period $\left(\frac{\text{W. R.}}{\text{E.}}\right)$ when platted (fig. 37) are likewise

found to be highest in the oak-brush type, intermediate in the aspen-fir type, and lowest in the spruce-fir type, the curves in the case of each species following in a general way the physiological temperature indices.

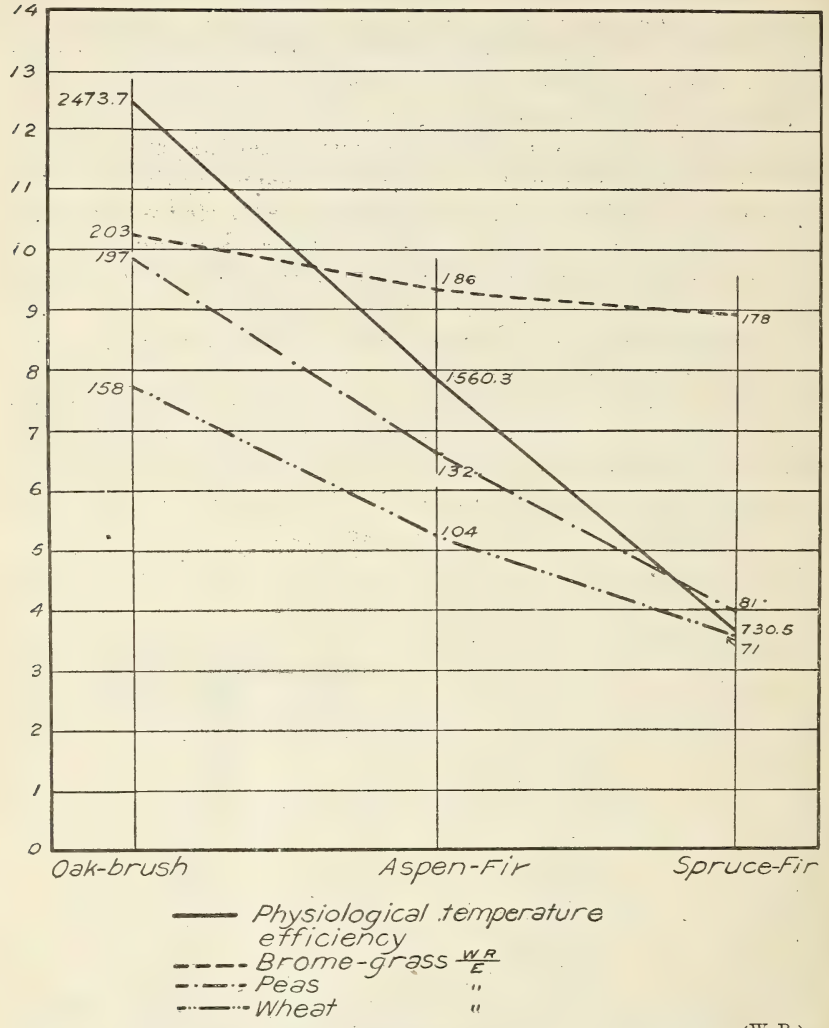


FIG. 37.—Relation of the quotient of water requirement and evaporation $\left(\frac{\text{W. R.}}{\text{E.}}\right)$ to temperature.

On the basis of the agreements shown, it may be concluded that the water requirement of these plants is determined largely by evaporation and temperature. Hence it is evident that in localities of limited rainfall, high evaporation, and high temperature values, agricultural pursuits, even where the most drought-resistant species

may be economically employed, should be confined to soils of high water-holding capacity and subject to minimum run-off, so that the soil may return to the plant a high percentage of the rainfall.

## SUMMARY.

The data reported, pertaining as they do (A) to the climatic characteristics of three distinct vegetative associations, (B) to comparative instrumentation and methods of summarizing and expressing climatic factors, and (C) to correlations between environmental factors and plant growth and other physiological activities, may best be summarized under three heads.

### A. CLIMATIC CHARACTERISTICS OF THE PLANT ASSOCIATIONS.

1. The mean annual temperature increases gradually from the highest to the lowest type, and this results in the longest growing season in the lowest type and a gradual decrease in the period of growth with increase in elevation. Thus from the time of the beginning of growth to the occurrence of killing frosts there are about 120 days in the oak-brush type, 105 in the aspen-fir type, and 70 in the spruce-fir type.

2. The normal annual precipitation is greatest in the aspen-fir association but is only slightly heavier in this association than in the spruce-fir. Less than half as much precipitation is recorded in the sagebrush-rabbit-brush as in the aspen-fir association; and in the oak-brush type it is only slightly greater than in the sagebrush-rabbit-brush type. The precipitation is rather uniformly distributed throughout the year.

3. Of the three associations critically studied, the evaporation during the main growing season is greatest in the oak-brush type; but owing to high wind velocity in the spruce-fir type the evaporation is nearly as great as in the oak-brush type. In the aspen-fir type the evaporation factor is notably less than in the types immediately above and below. This is accounted for largely by the lack of high wind velocity, which is due to the luxuriant vegetation and to topographic features.

4. The wind movement is greater by about 100 per cent in the spruce-fir association than in the types immediately below. Not uncommonly the velocity of the wind exceeds 40 miles per hour for several hours in succession. In the lower types the velocity averages slightly less than half that recorded in the spruce-fir type.

5. Sunshine duration and intensity are practically the same in all types studied.

6. There is considerable difference in barometric pressure in the respective types, but the daily seasonal fluctuations within a station are slight.

### B. COMPARATIVE INSTRUMENTATION AND METHODS OF SUMMARIZING EXPRESSIVE CLIMATIC FACTORS.

1. Temperature summations on a physiological basis according to the Lehenbauer plan have shown much promise in correlating air temperature with physiological plant activities. The summation of the effective temperature, namely, the temperature above 40° F., as proposed by Merriam, also appears to have much promise. This method in general compares favorably with temperature summations made on the physiological (Lehenbauer) basis.

2. Summations of average daily mean and seasonal mean temperatures appear to have little value in showing correlations between the factor in question and physiological activities in plants.

3. The evaporation for short periods, such as a part of a day or a fractional part of a week, for example, when compared with relative humidity, temperature, and wind velocity, can be obtained more accurately by means of the porous cup atmometer than by the free water surface evaporimeter of the Weather Bureau pattern. For periods of a week or longer either instrument will serve.

4. In recording sunshine as related to plant activities, both duration and intensity should be considered. Such records can be obtained approximately by noting the difference in evaporation between similarly exposed black and white porous cup atmometers. These instruments appear to have some advantages over the Marvin sunshine recorder, which furnishes a record only of sunshine duration.

### C. CORRELATIONS BETWEEN ENVIRONMENTAL FACTORS AND PLANT GROWTH.

1. Lack of uniformity in the fertility and, of course, in the texture of the soil in which the plants are grown may cause considerable variation in their water requirements and in the total dry matter produced. Soil collected within a restricted habitat often varies considerably in productivity, and unless thoroughly mixed may become an important source of error in experimentation.

2. The total effective heat units and length of growing season in the three types studied are such that only in the lowest association do crops like wheat and peas reach full maturity. Hence, farmers should not attempt locally to grow the ordinary agricultural crops, such as cereals, above an elevation of about 8,000 feet. The elevation at which there are normally sufficient heat units to develop and mature cereal crops in general varies, of course, with the latitude and longitude.

3. The rate of maturity of the plants decreases directly as the effective heat units decrease, as is the case in passing from the lowest to the highest type. This decrease in the rate of maturity of the plant in the type stations may be shown, up to a certain point, at

least, by the difference between the water requirements of the aerial parts of the plants, including the fruit or seeds (such as the heads of wheat), and of the aerial portion without the seeds, the specimens with the best developed seeds, of course, having the highest water requirements.

4. The water requirement for the production of a unit weight of dry matter is greatest in the oak-brush type, lowest in the aspen-fir type, and intermediate in the spruce-fir type. These relations coincide with the relative intensities of the evaporation.

5. In the case of all species employed, the total, and, indeed, the average leaf length and total dry weight produced are notably greatest in the aspen-fir association, these activities being rather similar in the spruce-fir and oak-brush types. The decreased production in leaf length and the production of dry matter in the respective types are in direct proportion to the evaporation.

6. The elongation of the stem is greatest in the oak-brush type, intermediate in the central type, and least in the aspen-fir type. Thus stem elongation appears to be determined largely by temperature and seems to be little influenced by the intensity of the evaporation.

7. The efficiency of the leaves per unit area as manufacturing agents—that is, in the production of dry matter, appears to vary inversely with the evaporation, though, indeed, temperature appears to be one of the important factors. The largest amount of dry matter per unit of leaf area is produced in the aspen-fir type and the least in the oak-brush type, while in the spruce-fir type, where the evaporation is only slightly less intensive than in the oak-brush type, the dry matter produced is only slightly greater than in the oak-brush type.

## CONCLUSIONS.

From the study here reported, it may be concluded that in this locality Kubanka wheat and Canadian field peas, and doubtless other agricultural crops, can not be grown profitably at elevations exceeding about 8,000 feet because of the lack of sufficient heat. As has been shown by the crop production of the region, enough heat units were produced in the seasons studied up to an altitude of about 8,000 feet, which includes most of the oak-brush type, to mature wheat, peas, and certain other crops. The amount of precipitation received at an elevation of 8,000 feet and lower, however, was below the requirements of crop production, indicating that the lands must either be irrigated or the moisture conserved by thorough summer fallowing. The native forage crop produced in the oak-brush type, on the other hand, is fairly luxuriant, and if properly utilized will

continue to be of high value in the pasturing of live stock. On the more favorable sites from the oak-brush up to and including the spruce-fir association, lands which have been overgrazed and are not fully stocked with vegetation may be increased in forage production by the seeding of suitable plants, preferably native species.[1]

Since evaporation is apparently the chief factor limiting growth and development of plants in the oak-brush and spruce-fir types, the extension of agriculture and forestry should be limited to lands protected from excessive evaporation. This may be done by selecting sites that are more or less protected by native vegetation and natural obstacles. Failures in experimental plantings, in most instances, have occurred on wind-swept lands where the soil moisture becomes deficient early in the season. In the selection of species, either of herbaceous or of woody plants, only the most drought resistant sorts should be used. Failures in the case of the planting of suitable timber species in the central (aspen-fir) type will probably seldom be caused by adverse climatic conditions. Failures in this type may generally be traced to the employment of unsuitable stock, or to bad workmanship, wrong season of planting, or other preventable causes.

[1] Sampson, Arthur W. Natural revegetation of range lands based upon growth requirements and life history of the vegetation. Journ. of Agr. Research, Vol. III, No. 2, 1914.

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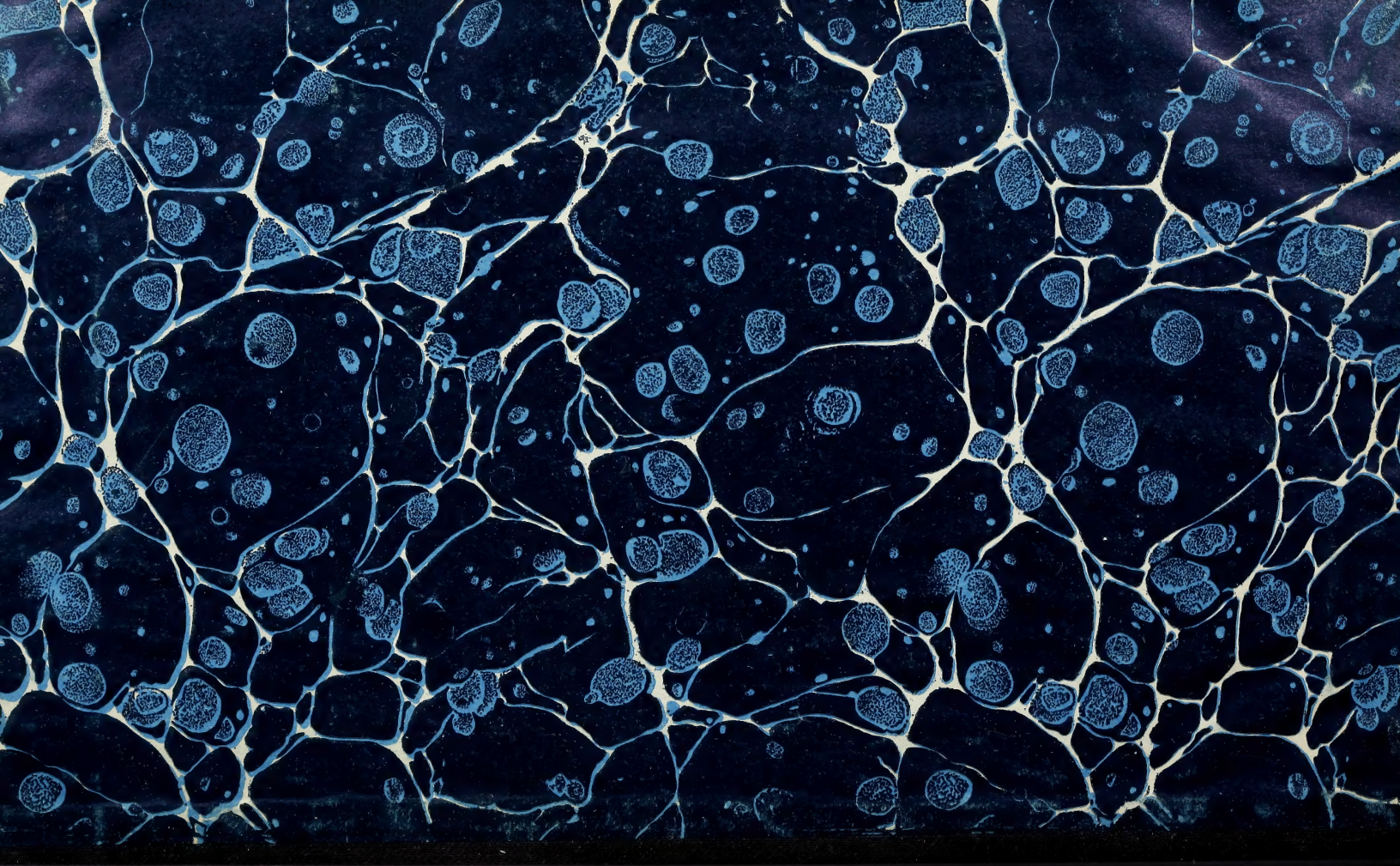

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